The Mechanisms and Processes of Vegetation Dynamics on Oil-Shale Spoil Bings in West Lothian, Scotland

(The West Lothian Question)

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Contents

Abstract

The work establishes the ecological importance of shale bings at both a local and global scale by presenting the mechanisms and processes of succession. The bings are post-industrial spoil heaps, the result of retorting mineral oil from deep-mined carboniferous shale beds.

The structure of vegetation on the shale bings was determined by a review of published data and a base-line survey of eight bings resulting in new floristic and environmental data from 340 quadrats and 261 plant species. The floristic data were analysed in the context of ecological indicator values (Ellenberg), functional type (competitive, stress-tolerant, ruderal), National Vegetation Classification and two-way indicator species analysis. The results indicated considerable variation in plant communities both between and within different bing sites.

The vegetation patterns were associated with the physical (altitude, aspect, slope and bare ground) and chemical (pH, calcium, phosphorus, potassium, magnesium, and nitrogen) environment of the shale substrate. Multivariate analyses (Detrended Correspondence Analysis and Canonical Correspondence Analysis) were used to ascertain the amount of species variation explained by each of the different environmental gradients. Although these abiotic environmental factors were shown to have a statistically significant influence on the plant community structure around 75% of the variation was still unaccounted for.

Nine species were selected to determine whether inherent plasticity within a species (plant height, number of flowering heads and seeds produced), the influences of seed dynamics and plant physiology could account for the variation in community structure not explained by environmental variables. This showed that almost half of the variation between and within bing sites was stochastic and probably dependent on the chance arrival of propagules in the initial stages of succession.

The results from this study were compared and contrasted with theoretical successional models and with similar studies of primary successions on both natural (glaciers, sand dunes, islands in fresh water, coral islands and volcanoes) and man-made (china clay, coal, other post-industrial sites, urban waste and arable land) sites. The similarities established the relevance of the work to other regions and sites, to successional theory and to ecological restoration and management practices.

On a local scale the bings are shown to have high ecological importance. They are refugia for locally rare fauna and flora and are a major component of the West Lothian biodiversity action plans. They are also of considerable social and historic importance.

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To anyone who I have forgotten to name, apologies and thank you - put it down to a "senior moment".

CHAPTER ONE

"The ecosystems which appear naturally on derelict land, without human assistance, are of considerable interest... they tell us about processes of ecosystem reconstruction and also about natural ecosystem development."

A.D. Bradshaw (1983). Presidential address to the British Ecological Society, December 1982.

1 Introduction

The importance of understanding the mechanisms and processes of colonisation and vegetation dynamics has long been recognised as a major factor in interpreting the development of plant communities. Only rarely does the opportunity arise to study colonisation on a primary succession site that is previously unresearched. The oil-shale bings of West Lothian provide such an opportunity. The shale bings, like all spoil heaps and quarries, start as sterile environments, with no previous vegetation or existing seedbank; therefore colonisation by plants and the subsequent development of vegetation is a primary succession. There are few naturally occurring sites where primary succession can be studied. This rare man-made habitat offers an environment against which accepted models of colonisation and their components can be tested.

The West Lothian shale bings are vast heaps of spoil, the waste product of the paraffin industry in Scotland. From the mid -19th to the mid - 20th century crude oil was produced in West Lothian by retorting locally mined oil-bearing shale and it is the discarded, burnt shale that forms the substrate of the bings. The individual bings vary in size, age and contain examples of both managed and unmanaged sites (Chapter Two and Appendix 1). Although the oil-shale bings are man-made, the plant communities and patterns of vegetation found there represent a range of seral and temporal stages within primary succession.

1.1 Ecological Importance of the West Lothian Bings

The shale bings are of great ecological and scientific importance as examples of primary succession and vegetation dynamics. The bings are unique in the United Kingdom. Oil-shale spoil is physically and chemically different from other spoil types making predictions from research on other spoil sites difficult and unreliable (Chapter Four). Many of the sites have remained unmanaged since shale extraction ceased and are slowly being colonised by plants and animals. Others have been reshaped, seeded and planted in various ways during the 1970's and 80's when land reclamation was "fashionable". The resulting vegetation, in both instances, is unique and varied. Their heterogeneity, both between and within sites provides a wide range of habitat conditions for the study of colonisation processes and the ecology of individual species that are adapted to low competition high stress conditions.

1.1.1 Importance of the bings to West Lothian

Formal recording of plant and animal species presence has been carried out on most of the bings although there is no published data on abundance, distribution or community structure. There has been little research in any scientific discipline on the bings and many of them appear only as vague outlines on topographical maps. Despite this, the potential value of some of the sites as habitats for locally rare species has been recognised (Chapter Seven) and they now have some degree of protection. The oil-shale bings form one of the eight main habitats in West Lothian's Local Biodiversity Action Plan (Sheldon, 1997). The bing habitats vary from almost bare substrate to semi-natural grassland, heather scrub and pioneering birch woodland, providing refuges for a range of animals and plants that are under increasing pressure in surrounding agricultural and urban areas.

1.1.2 Global importance of the bings

On a global scale the recent renewal of interest in oil extraction from shale is likely to lead to an increase in the volume of oil-shale spoil, particularly in the United States of America. Public opinion and government policy in many countries now demand that sites degraded by industrial processes should be restored to acceptable levels of "naturalness". To be able to comply with this it is necessary to achieve

ecosystems on oil-shale spoil that are self sustaining, are developed economically, possess the species and structure desired, control erosion, and form a safe and socially acceptable landscape. The West Lothian shale bings provide indicators for management and reclamation best practises.

1.2 Aims

The aim of this thesis is to identify the mechanisms and processes that determine the development of plant communities during succession and explain the processes driving vegetation dynamics. This has been addressed by experimentation, investigation, enquiry and analysis of new data collected from the study of vegetation on oil-shale bings in West Lothian, Scotland. The resulting information is used to test a range of successional models from literature and to produce a succession model of vegetation dynamics on the bings. Species traits from the bing vegetation are then compared with those from vegetation in other primary sites.

In any research involving the study of biological processes in a man made environment it is important to understand the historical background to its ecological status as well as a detailed knowledge of the particular aspects being studied. The following sections of this chapter briefly review methods of analysing and describing vegetation, the theories of succession, the mechanisms and processes of succession, other mechanisms and processes effecting vegetation dynamics, and previous research on other types of spoil and natural primary succession sites. A series of questions (Section 1.7) addresses how succession models proposed in the literature might be tested using information from the bing sites. In Chapter Two the geological processes that formed the oil-bearing shale strata are described, the physical and political geography of the study area is defined and a brief history of the shale-oil industry is outlined. Individual reports on the various aspects of the research are presented in later chapters.

1.3 Analyses and Statistics

Various methods of classifying and describing vegetation and plant communities can be found in literature (Grime, 1974; Silverton *et al.*, 1992; Harper, 1982; Peterken,

1974; Shimwell, 1971; Greig-Smith, 1983; Rees and Bergelson, 1997; Tilman, 1988; Austin 1977; Rodwell, 1991a; 1991b; 1992; 1995; 2000). Analytical and statistical methods are dependent on the types of data being used and the questions being posed.

Community ecology is studied on a wide range of temporal and spatial scales, from millimetres to kilometres and from days to centuries (Gauch, 1982). Even when studying the ecology of a single species more than one characteristic will be measured and the relationships between these characteristics need to be studied simultaneously. Community ecology field data are noisy because, although numerous species abundancies are controlled by a relatively small number of environmental and historical factors, each species is individual and each site and environmental factor is, to some degree, unique. A range of multivariate strategies have been developed, providing the ecologist with the tools required to analyse, format and present data by three basic methods depending on whether the emphasis is to be on aspects of community structure or relation to the environment.

1.3.1 Direct gradient analysis (DGA)

This is used to study the distribution of species along recognised, easily measured, environmental gradients. Plant communities are not a random assemblage of plants. Their composition is dependent on a wide range of factors, both biotic and abiotic. Classification and description methods frequently group plant species together by environmental and/or resource gradients (Ellenberg, 1988; Hodgson, *et al.*, 1995). These can be indirect environmental gradients (altitude, aspect and slope) or direct environmental gradients (pH and temperature) as described by Austin (1972; 1977), and Austin and Smith (1989). These methodologies are often based on the established phase of the life history of individual species within a community and may not be directly transferable to the developing vegetation on the bing sites being studied. The purpose of direct gradient analysis is to gather and organise community and environmental data in a quantitative way. It determines which environmental factors(s) principally affect(s) the distribution of organisms and communities within

the study area, which factors are secondary to this distribution and whether the communities are discrete and well defined or follow a continuum (Gauch, 1982).

1.3.2 Ordination

Ordination is used when the main emphasis is on community structure or when environmental data are not available. It places similar entities in proximity with each other by a range of techniques. These include weighted averages, principal components analysis (PCA), reciprocal averaging, detrended correspondence analysis (DCA), and canonical correlation analysis (CCA). Ordination is effective for showing relationships, reducing noise, identifying outliers and disjunctions, and presents the data in terms of community composition. This may or may not relate to environmental factors. Ordination is commonly used in the study of succession and other floristic analyses (Austin, 1977; Daniels, 1978; Wildi, 1988).

1.3.3 Frequentist statistics

Ecological community field data are not usually suitable for statistical methods of analysis. Standard frequentist statistics are, however, used on the results of ordination and other multivariate analyses to determine the probability of a null hypothesis (e.g. there is no relationship between vegetation communities and altitude). They can also be used to test the non-randomness of occurrence of groups of species (e.g. Monte Carlo Analysis). A wide range of frequentist statistics is recognised as standard analytical tools and is necessary to describe the results of experimental data. T-tests, Chi-squared, Mann-Whitney, Anova, Regressions, F-test and many others can be selected to show the statistical significance of the outcomes of research.

1.3.4 Bayesian statistics

The Bayesian approach to statistics is a relative newcomer to Ecology although it is based on Bayes' Rule and derived from a problem[1] expressed more than 240 years

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[1] *Given* the number of times in which an unknown event has happened and failed: *Required* the chance that the probability of its happening in a single trial lies somewhere between any two degrees of probability that can be named.

ago (Bayes, 1763). Bayesian statistics were subsequently developed by, among others, Jeffreys (1934; 1937) but the theory was suppressed for most of the 20th Century by frequentist statisticians. The main problem facing the ecologist is that the Bayesian method of analysis can not just be added to the range of statistical methods already used. Bayesian statistics, or inverse probability statistics, involve substantial changes to the methods and philosophy of science and are largely untested. This type of analysis has been used to predict the outcome of plant competition experiments with some degree of success (Damgaard, 1998; Pascual and Kareiva, 1996), but its general use is very much under discussion (Dennis, 1996).

1.4 Succession - The Mechanisms and Processes

The changing patterns of vegetation on land have been recognised from the earliest periods in human history, indeed farmers have used this knowledge to maintain cyclical crop production (slash and burn) since agriculture began. King (1685) is reputed to have presented the first scientific study of succession when he described Irish bog vegetation for Philosophical Transactions and the term "succession" was first used, in its present ecological sense, by the French biologist Dureau de la Malle (1825). A review of 21 key papers tracing the development of ecological succession theory from Cowles (1901) to Drury and Nisbet (1973), including reprints of many of them, has been published as volume five of the Benchmark Papers in Ecology series (Golley, 1977). From this it was possible to compile a generic model of the sequence of succession that the bing vegetation would be expected to follow. Succession can be divided into two main categories, primary succession and secondary, or subsequent, succession. Primary succession develops on a completely sterile environment with no previous vegetation. Secondary succession develops after disturbance on previously vegetated land. Literature suggests that the mechanics and processes of both primary and later successions follow similar overall sequences from invasion to stabilisation.

1. Invasion: In both primary and later successions invasion is the initial arrival of seeds and spores on an unvegetated substrate. These may already be in the seedbank (dispersal through time) after the loss of previous vegetation or may

arrive by dispersal from the surrounding area (dispersal through space) (Grubb, 1987). The success of invasion is dependent on seed and spore availability, dispersal characteristics, wind direction, animal activity and entrapment (surface roughness). As the bings are primary sites the vegetation is expected to reflect that found in the surrounding landscape: the nearest seed source.

2. Ecesis: Availability of a large number of seeds does not presuppose germination. Of the seed species represented only some will germinate and of these varying percentages of individual species will reach the seedling stage (Fenner, 1985). Fenner (1987), and Eriksson and Eriksson (1998) suggest that seed dormancy in some species may increase the potential for successful germination and establishment, as may seed size and morphology (Guo, *et al.*, 2000; Funes, *et al.*, 1999). It is unlikely that these will be major deciding factors in the spatial distribution of seedlings on shale bings as it is recognised that the effectiveness of these strategies is strongly linked to competition intensity (Eriksson and Eriksson, 1998). The microsites where seeds are trapped must be conducive to germination and establishment. Early colonising plants, particularly in a primary succession, must be able to acquire ample nutrients and water without mycorrhizal associations (Johnson, 1998) as sterile environments, like oil-shale bings, are depauperate in mycorrhizal propagules. Many of the germinating species will not be suited to the bing habitat and will survive only for a short time as transients (section 1.6 paragraph 1).
3. Survival: As mentioned in the previous paragraph germination and the establishment of seedlings are not synonymous with plant survival. While a continuing supply of water and nutrients is required, long-term survival is also dependent on levels of soil fertility, pH, light and moisture, falling within limited ranges for individual plant species, as described by Ellenberg (1988). Excess amounts of soluble salts, such as are reportedly found on oil-shale spoil (Bradshaw and Chadwick, 1980), and heavy metals are toxic to many species. The physiological features of individual species, like leaf size, plant height, mechanical and chemical protection against grazing, and clonal colonising ability will all be important factors contributing to survival and population growth.

4. Reproduction: Continued invasion of species is by seed dispersal from locally established vegetation and from neighbouring areas and is dependent on the reproductive output of individual plants and population size. Reproduction is a function of the number of flowering heads, length of flowering time, availability of pollinators, number of seeds produced, vegetative spread, and the viability, longevity and dormancy of seeds. Varying seed production between and within individual species is a major determinant of the ratios of species within plant communities, seedbanks and seed rain. The fecundity of locally available species suited to the shale bing habitats will be a primary contributor to their colonising success, both spatially and temporally, and to the overall vegetation structure.
5. Pre-emption: Stochastic elements will play a large part in determining the initial floristics of the sites and any subsequent changes in community structures (Harper, 1982; Rees and Bergelson, 1997; Miles, 1973). It is a matter of chance which species arrive first in any new environment. The growth strategies of these first colonisers can inhibit or facilitate colonisation by later arrivals. Extreme pre-emption can result in an initial flora of a few species that are easily replaced or a completely non-invasible plant community. The full importance of initial floristics and transitory species in determining the outcome of competition and community structure remains an as yet unresolved question in community ecology (Rees and Bergelson, 1997). It is hoped that this study of the vegetation processes on the shale bings will begin to address the issue.
6. Changes in resource gradients: As mentioned earlier in this chapter (introductory paragraph) there is a wide range of variation in the height, basal area and age of the bing sites in this study (Appendix 1). The greatest distance between any two bings is 7 kilometres and all 19 lie within a 10-kilometre radius. This makes them ideal for recording changes in resource gradients, which can occur both over time and spatially. These changes can be caused by existing vegetation, by topographical and climatic components or a combination of these.
7. Competition: In the initial stages of succession competition is absent when pioneers are still isolated but it increases with the increase in population in successive stages. It is not expected to be a major factor in areas of the bings with low vegetation cover. Competition can be for light, moisture, air and

nutrients. Clements (1916) states that "Competition occurs whenever two or more plants make demands in excess of the supply." These plants can be from the same or different species. Competition effects are greatest between individuals or species with the same or similar requirements for resources and least between associated plants with differing demands. They are often most consequential during the stages of ecesis (section 1.4 paragraph 2) when closely dispersed seeds from one species develop into numerous seedlings, each with identical demands on the same limited resources.

8. Interactions: Inter- and intra-specific interactions are not always competitive (although competition is an interaction). Within many developing plant communities, like those found on the bing site, species and individuals in a mixed population will survive better than those growing in a single species stand. Pioneers often act as nurse plants to other invading species, with much benefit to the latter but at no cost to the former. The relation between trees and herbs in a community is non-competitive because species in lower layers of vegetation are adapted to the conditions imposed on them and in many cases benefit from shading or other factors.

1.5 Other Mechanisms and Processes

Mechanisms and processes that do not fall into any one of the succession categories will have varying degrees of influence on the overall patterns and dynamics of developing vegetation at both species and community level.

1. Plasticity: Plasticity and intra-specific variation play an important part in the ability of individual plants to compete within a population or community. This is particularly true of weed species (Harper, 1960; Harper, 1977; Gray, 1993) and is likely to be a predominant factor in the early successional vegetation of the shale bings. The significance of relative growth rate and plasticity in relation to competition has been recognised by many as an important element of ecophysiology (Burdon and Harper, 1980; Jefferies *et al.*, 1981; Parsons, 1968; Tilman, 1985; Shipley and Parent, 1991; Marañón and Grubb, 1993; Peltzer, 1999).

2. Climate: Annual and seasonal changes in temperature, rainfall and hours of solar radiation all have a direct effect on seed production, germination, establishment and growth in plants. Even minor changes of climate can cause large-scale increases or decreases in the populations of individual species. The possible affects of global warming on Scotland are the subject of fierce debate making the consequence of any subsequent climate change on the succession patterns of the shale bings unpredictable and completely outwith the remit of this study.

1.6 Other Influences Affecting Plant Community Structures

Several factors that determine plant community structure are external or temporary influences and do not fall into the categories of mechanisms or processes. These are animal behaviours or plant strategies that directly govern the efficacy of elements of the succession process. Transient, transitory and uncommon species from surrounding landscapes are constituents of the earliest stages of all successions. Their effect on a new landscape and the advantages that such a site offers them are frequently ignored in the investigation of colonisation.

1. Transients: These are plant species (sometimes called ephemerals) that are not lasting or durable, whose seeds invade an ecosystem, germinate and establish but only rarely survive to reproduce. Transients are often relatively abundant species from nearby ecosystems that are unsuited to the physical and/or chemical conditions in their new environment. They are likely to be important in the development and maintenance of the ecosystem (Grime, 1998) by adding more nutrients and organic matter to the soil than they extract. They are representative of the assortment of potential later colonisers and are important to the continuing biodiversity of a community in subsequent successional stages.
2. Transitory species: Transitory species are species that form an integral part of one or more of the early stages of succession. These are species whose ecological niche is to move from one disturbed site to another. They reproduce and are well adapted to the initial conditions of the new environment. However as the ecosystem develops they are less able to compete with new invaders, or are unable to adapt to the physical and chemical changes in the developing substrate.

3. Uncommon species: These are usually native plant and animal species that are living at the edge of their preferred habitat range and are out competed by other, better suited species. An island refuge, like a shale bing, that provides a new habitat can potentially be of great importance to these species by providing a more amenable environment. Plant species that struggle to survive on the surrounding arable land may be the best adapted for the physical and chemical conditions found on shale bing substrate. They can also become an integral part of plant communities in later stages of succession as conditions suitable for their establishment, survival and reproduction develop (Grime, 1998).
4. Animal behaviours: Plant parasites, herbivores, predators and symbionts make ecosystem impact by vegetation less predictably related to abundance. Their effects are not investigated in this thesis, but any relevant observations resulting from survey and experimental data sets has been recorded and discussed.

1.7 Previous Research on Primary Succession Sites

There has been considerable research on primary substrates of various types throughout the United Kingdom and the rest of the World. The processes and mechanisms producing patterns of vegetation are generally accepted as being the same for all primary succession sites (Section 1.4), both natural and man-made. The physical properties of their substrates are similar (Chapters Three and Seven), although the chemical properties are more diverse (Chapter Four). Climate reflects the different geographical locations of sites, and plant species and communities will vary accordingly, but the growth traits and characteristics of many species should be comparable between distinct types of site.

1.7.1 Man made primary succession sites

These are many and varied. The most obvious are often the result of mining and quarrying for minerals. In the United Kingdom such sites were largely ignored until the 1960's and 70's when a nation wide, demolition, reclamation and restoration plan attempted to reproduce varying degrees of "naturalness" to the devastated landscapes. It was only when sites were surveyed to determine management strategies that their scientific and ecological importance was fully recognised

(introductory paragraph). The information collected from studies made on the oil-shale bings for this thesis will be compared with findings from other studies in primary succession sites in Chapter Six.

1. Oil-shale waste: There has been little research on succession, vegetation dynamics or plant communities on oil shale spoil, or on the mechanisms and processes determining the structure of the resulting vegetation in these communities. There are descriptive accounts of the vegetation (Maka, 1995; Martin 1992) and the development of both soil and vegetation (Russell, 1971) on some of the West Lothian oil-shale bings. West Lothian Council archives have a range of reports and documents relating to Drumshoreland, Seafield, Oakbank, Addiewell south and Mid Breich bings; including details of any remedial work that have been carried out from 1967 onwards (West Lothian Council, various dates). A detailed description of the physical and chemical structure of shale spoil is included in Chapter Five and a brief history and description of each bing has been compiled in Appendix 1.
2. Coal spoil: The plant communities, physics and chemistry of coal spoil, from both strip and deep mining, have been studied in many parts of the world (Allen and Allen, 1980; Jefferies *et al.*, 1981; Fyles *et al.*, 1985; Palmer and Chadwick, 1985). For example, Allen and Allen (1980) demonstrate that the earliest successional plants in reclaimed strip mines (coal) do not form mycorrhizal associations, as the acid substrate of coal spoil is low in mycorrhizal inoculum. They suggest that the lack of mycorrhizal inoculum is likely to inhibit later colonisation by mycotrophic species. It is not known if a similar range of species forms the basis of early successional vegetation on shale substrate, which is more alkaline.
3. China clay: Ecosystem development on reclaimed china clay waste in southern England has been researched and reported in a series of papers from the University of Liverpool (Marrs, Granlund and Bradshaw, 1980; Marrs and Bradshaw, 1980; Roberts *et al.*, 1980; Marrs, Roberts and Bradshaw, 1980). In these studies sixty-eight sites were surveyed to assess the vegetation and to quantify the cycling of nutrients (with emphasis on nitrogen): particularly capture

by, compartmentation in and leaching from the above ground plant material. The works concentrated on the importance of resource acquisition in the invasion by and development of vegetation. Is this a more significant factor than the proximity of seed sources and their dispersal mechanisms in determining the development of plant communities on spoil?

4. Derelict land sites: Considerable research has also been documented on succession and vegetation development in quarries and gravel pits (Davis, 1982; Gray, 1982; Borgegård, 1990; Myster and Sarmiento, 1998). The general processes of vegetation on derelict land have been described many times (for example Tandy, 1975; Greenwood and Gemmell, 1978; Bradshaw and Chadwick, 1980 and others).

1.7.2 Natural primary succession sites

Volcanoes, sand dunes and glacier moraines are some of the naturally occurring substrates where primary succession has been studied. Bradshaw (1983) describes spoil left after mining as similar to that formed by these natural processes and Cadell (1925) compares the West Lothian bings to volcanoes. In contrast to the man made primary sites, many of these natural sites have been the subjects of studies over many decades, even centuries, and large, comprehensive, descriptive, data sets have been published.

1. Volcanoes: There have been several long-term studies on the development of vegetation in the aftermath of volcanic activity on the Krakatau island group, Indonesia (Ernst, 1908; van Borssum Waalkes, 1960; Bush et al., 1983; Bush and Whittaker, 1991; Partomihardjo et al., 1992; Whittaker et al., 1989; Whittaker and Bush, 1993). More recently studies have been made on the mechanisms of primary succession on Mount Vesuvius, Italy (Mazzoleni and Ricciardi, 1993) and Mount St. Helens, United States (del Moral, 1993).
2. Glaciers: Similar studies have described the development of vegetation on the forelands of receding glaciers from all over the world. Long term studies in Glacier Bay, Alaska by Cooper (1923a; 1923b; 1923c) relate 20th century vegetation patterns to tracts of land uncovered during the early stages of long term glacier retreat, starting before 1794. These studies compare the primary

succession patterns of plant communities in areas more recently (sic) uncovered by the same glacial retreat. Crouch (1993) documented the species composition of 190 sites in, and alongside, forelands in Southern Norway, recording both cryptogams and higher plants. The effects of species of willow on the establishment and survival of indigenous plants was tested on Lyman Glacier forefront in Washington (Jumpponen et al., 1998). Schlag and Erschbamer (2000) conducted experiments on seedling germination and establishment on a glacier foreland in the Austrian Alps.

3. Sand dunes: Cowles (1899a; 1899b; 1899c; 1899d) studied the plant ecology of the sand dunes on Lake Michigan in one of the first, documented examples of vegetation succession. In this series of four papers he describes, among many other mechanisms, the positive effects of facilitation by early successional species on the establishment of later colonisers. The rates of succession on the same sand dune systems were investigated by Olson (1958) and used in experimental studies to develop ecological knowledge of primary and secondary succession (Lichter, 2000).

1.8 The Questions

The following questions relate to the bing vegetation and to models of successional mechanisms and processes that have been proposed by various authors. Each of these will be addressed in more detail in later chapters, both in the context of the literature and in the light of current research.

1. Vegetation structure: Are there recognisable patterns in the bing vegetation? Do species invade from the immediately surrounding plant communities? Does species diversity increase with the age of the bings? Will the first colonisers be cryptogams, followed by grasses and herbs? Will the species composition be dictated by stochastic events or as a result of deterministic processes? Are the resulting species associations representative of recognised plant communities in the United Kingdom? (Chapter Three)
2. Environmental gradients: Are vegetation patterns associated with environmental gradients? How limiting is the absence of soil, in the biological sense, to the

colonisation process on shale bings? Does species composition reflect gradients in either the chemical or physical environment? (Chapter Four)

3. Seed dynamics and interspecific plasticity: How great a determining factor in the establishment of vegetation is the availability of seeds and spores in seed rain and the seedbank? Is phenotypic plasticity a major contributor to vegetation dynamics at individual species level? Will local site conditions have a direct effect on the size of individual plants, measured as height above ground, and hence on the number of flower heads and seeds produced? Is any variation in seed production within a species correlated with either height or number of flower heads? (Chapter Five)
4. Succession and other primary sites: Do bings provide acceptable models of primary succession? Does succession on shale bings follow previously identified 'rules'? Do the patterns of succession follow the same trends as those recorded on other primary sites, both natural and man-made? Does the vegetation on oil-shale bings develop in an analogous way to other island communities, particularly those found on volcanoes and oceanic islands? (Chapter Six)
5. Ecological value: what is the ecological value of the study of colonisation on shale-bings? Can indicator species be used to identify the physical and chemical structure of the substrate? How important are transient species to the establishment of plant communities? Are the examples of both assisted and natural colonisation processes and mechanisms on bings relevant to the restoration and management of other spoil sites? What effect do spoil sites have on local biodiversity? (Chapter Seven)

CHAPTER TWO

"History belongs not only to those who made it, but to those who inherit it"

Alistair Finlay (1999). Shale Voices (preface). Luath Press Limited, Edinburgh.

2 West Lothian, Oil Shale and the Shale-oil Industry

The county of West Lothian and its shale bings are unique within the United Kingdom making it necessary to include some background information on various features of their origins.

2.1 The Geography of the County

West Lothian, the second smallest of Scotland's mainland counties (after Clackmannanshire), is located on the southern shore of the River Forth, in the middle of central Scotland between Glasgow and Edinburgh (Hendrie, 1986). The area of land which it now encompasses was, for many centuries, most of Linlithgowshire and part of Edinburghshire (Ordnance Survey, 1987a; 1987b): later to be renamed West Lothian and Mid Lothian. After some major boundary changes in 1975 the modern day West Lothian was created as a district of Lothian Region (Tranter, 1979) but since April 1996 has been a 'new unitary authority' (West Lothian Council, undated). The present political boundary encloses 414 square kilometres (160 square miles) of land.

The main towns are Linlithgow, Torphichen, Bathgate, Armadale, Broxburn, Uphall, East-, Mid-, and West Calder, Bo'ness (Borrowstounness), Blackburn, Whitburn and Livingston, the fourth of Scotland's New Towns (1962) and the largest population centre in the Lothians, after Edinburgh (Tranter, 1979).

2.2 The Geology

The whole of central Scotland lies in a large rift valley formed between the Highland Boundary and Southern Upland faults. During the Old Red Sandstone Period (410 –

360 million years ago) the rift began to fill with debris from the newly risen Caledonian Mountains and accumulated over 50 million years. This was a time of extensive volcanic activity resulting in the formation of the Pentland Hills. The era was followed by the Carboniferous Period, when Scotland lay on the Equator and experienced a tropical climate (360 – 285 million years ago). At both the beginning and end of the Carboniferous there were again considerable plutonic activities, resulting in the rock formations at Arthur's Seat, and Salisbury Crags in Edinburgh, the Bass Rock, in the Forth Estuary and Berwick Law. Binnie Crag, Dechmont Law and other volcanoes and sills in West Lothian were the result of the same activities (Cadell, 1925).

Between the two periods of volcanic activity, warm seawater flooded across the central Scotland valley in a vast tropical lagoon; limestones developed from coral reefs and a host of organisms (including sharks and amphibians) were preserved as fossils in the silt of the lagoon basin. The land at the edge of this expanse of water was a swamp of primitive plants, which over time turned into coal under great thicknesses of sandstone. In the centre of the lagoon, layer upon layer of fine silt and plant debris were deposited by the tides to form oil-shale (Cadell, 1925). *Westlothiana lizziae* (also known as 'Lizzie'), the oldest known fossil lizard in the world, was discovered in the Calderwood shales near Bathgate by professional collector Stanley Wood in 1989 (Smithson, *et al.*, 1994; Smithson and Rolfe, 1990). At the end of the Carboniferous Period the strata of the central Scotland valley were folded from the pressure of new, developing mountains to the north, causing the coal and shale deposits to be twisted into the formations we find today (Figure 2.1).

Scotland continued to slowly drift northward during the Permian, Triassic and Tertiary periods (from 245 – 5 million years ago). New Red Sandstone developing from dry dune formations during the Tertiary period was deposited in the new folds of the central Scotland valley. The deposition of glacial tills and scouring by glaciers and ice melt caused by three major glacial advances over Scotland between 50 million and 10,000 years ago, plus an easterly tilting of the whole landmass, have left a heterogeneous mixture of rocks and minerals in central Scotland (Cadell, 1925). West Lothian has inherited (from west to east) bands of coal, fireclay, cement

limestone, sandstone, limestone and oil-shale covered by a rich glacial till. The present landscape of the county, apart from a small part of the coastal belt, is a record of exploitation of the land and its riches, both agricultural and industrial.

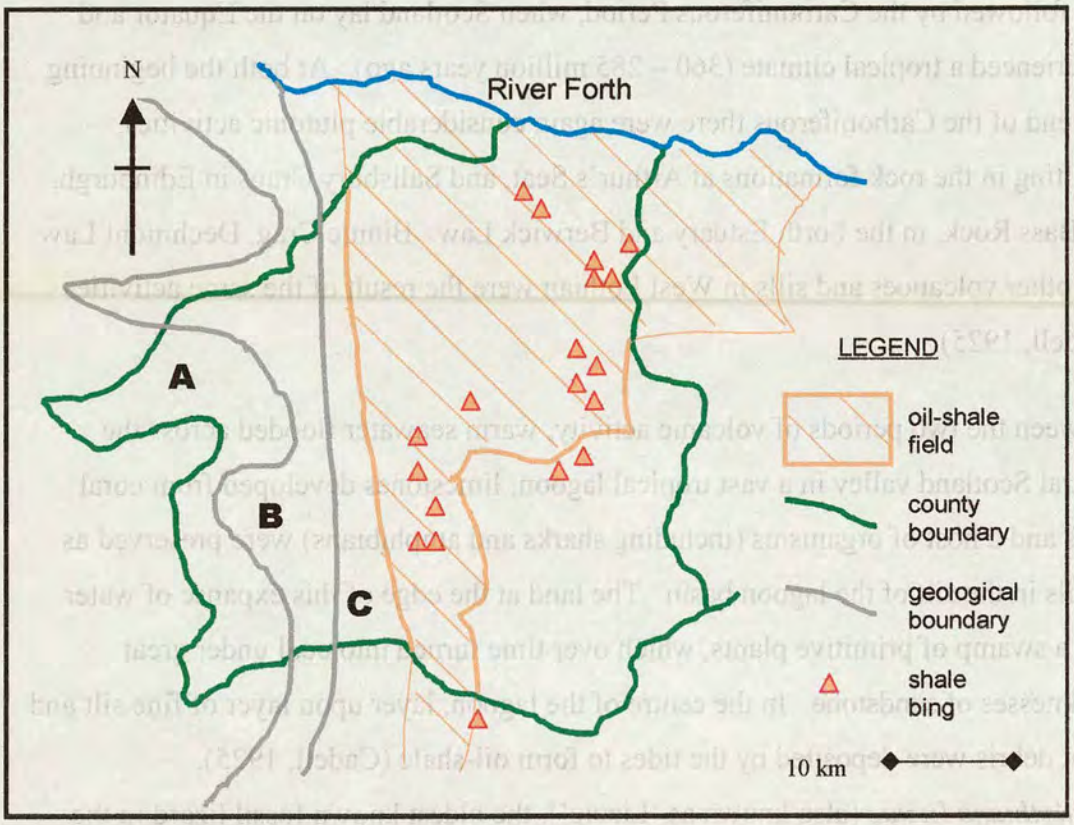


Figure 2.1 Geological Map of West Lothian

Simplified geological map of West Lothian (adapted from Institute of Geological Sciences, 1979 and Sheldon, 1997).

A: Westphalian coal measures; these extend west through Lanarkshire.

B: Millstone grit series; the source of fireclay

C: Carboniferous limestone series; formed of narrow bands of limestone and sandstone

2.3 The History

The history of West Lothian has been somewhat overshadowed by that of its larger neighbour, Edinburgh, however there have been settlements in the area since prehistoric times. Although largely an agricultural county, at various times in its history West Lothian has been mined for the diverse mineral deposits under its rich glacial till (Tranter, 1979; Hendrie, 1986; Colledge, undated). Coal was first mined

by monks at Carriden in 1165 (Cadell, 1925). Other major industrial operations included mining for ironstone, limestone, fireclay and shale. Slate was quarried at Mid Calder, and sandstone from Binnie quarries provided the yellow stone for most of Edinburgh's New Town (including the National Galleries, Register House and the Scott Monument). Even silver was mined in the Bathgate Hills from 1607 until 1614, when King James VI decreed that all proceeds were to go to Crown; at this point all the seams immediately "ran out". The silver mines were never mined for silver again but when the old workings were surveyed in 1873, nickel ore was discovered in the waste heaps and mining recommenced (Cadell, 1925; Hendrie, 1986; Tranter, 1979; Keay & Keay, 1994).

2.4 The Shale Oil Industry

An industrial process to extract crude oil from shale was first patented in 1694 in Britain. The first commercial plants were built in France in 1838 and Scotland (West Lothian) in 1851 (McHenry, 1992). Also in 1851, James "Paraffin" Young (1811-1883) (Figure 2.2) patented a new method of retorting paraffin oil from Cannell coal and oil bearing shale and built the first paraffin works at Boghall (Bathgate). This changed the face of West Lothian (Tranter, 1979; Hendrie, 1986; Colledge, undated).

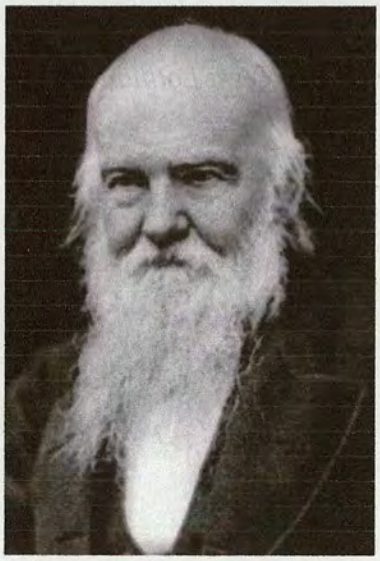


Figure 2.2 James "Paraffin" Young (1811-1883)

Founder of the Scottish oil industry in 1851 (photograph courtesy of "The Scotsman" newspaper archives).

2.4.1 The global picture

On a global scale, oil extraction plants were built in Australia, Brazil and the United States of America by the late 19th century, and by the early 20th century, China (Manchuria), Estonia, New Zealand, South Africa, Spain, Sweden and Switzerland were also producing oil from shale. Most production stopped by mid-century due to the discovery of large supplies of crude oil in the Middle East, although Estonia and Manchuria still operate commercial paraffin extraction plants (McHenry, 1992; Cadell, 1925).

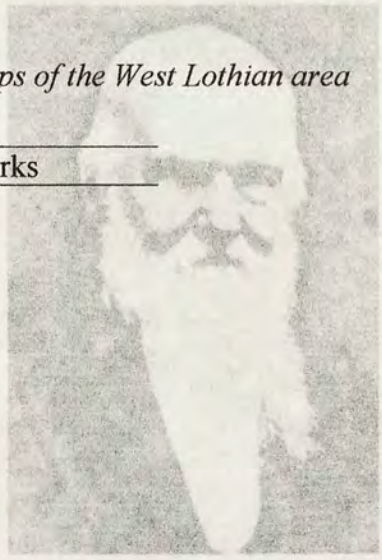
2.4.2 The importance of the industry in West Lothian

In West Lothian, James Young opened the original paraffin works using oil extracted from Cannel (parrot) coal but the seam soon ran out and no other Cannel coal was available locally. However oil-bearing shale was discovered near Broxburn and West Calder in 1858 and Young discovered that paraffin oil was also extractable from this source. He patented the process and crude oil was retorted at Westwood and Winchburgh then refined at Pumpherston into the paraffin oil that earned him his nickname, "Paraffin" Young. The patent ran out in 1864 leading to a massive increase in industrial workings (Tranter, 1979; Cadell, 1925) (Table 2.1).

Table 2.1 Industrial workings

The industries and works shown on Ordnance Survey maps of the West Lothian area (Ordnance Survey, 1987a; 1987b; 1957).

Type of industry	No. of works
Iron mine	1
Coal mine	16
Iron works	1
Coke oven	1
Stone quarry	9
Shale mine	14
Brick works	1
Oil works	9
Chemical works	1
Chemical factory	1
Unspecified mines/works	77



This is a huge under representation of the extent of these industries, as only those commercial plants based outwith the towns are recorded. By 1865 there were 120 oil works in operation in the county, alongside their associated shale pits and mines, producing 25,000,000 gallons (@ 600,000 barrels) of crude oil every year and employing 30-40,000 people (Hendrie, 1986).

Miners streamed into West Lothian from Cornwall, Wales, Ireland, the North of England and all quarters of Scotland. Towns and villages expanded rapidly causing the county to resemble the American Wild West. Gunpowder was produced at Camilty Powder Mill near Harburn and sold to shale miners (who had to supply their own explosives) in blue paper twists for 2d. Complete new villages grew up around the shale mines at Winchburgh, Niddrie, Seafield, Oakbank and Addiewell (Tranter, 1979; Hendrie, 1986).

Soon imported American oil was cheaper than the home manufactured product but by this time shale oil was used to produce motor spirit, naphtha, diesel oil, paraffin wax, petroleum jelly, wax for beekeepers, fluid for powering lighthouse lamps and detergent. By products were produced at the chemical works in Broxburn and Bathgate, including ammonia, sulphuric acid, mothballs, paints, rubber goods and candles (Tranter, 1979; Cadell, 1925; Hendrie, 1986; Keay and Keay, 1994). West Lothian was booming.

The maximum output from the industry was in 1913, when 3.5 million tons (27,125,000 barrels) of crude oil was produced. There was a gradual reduction in operations until, by 1951, output was reduced to only 1.5 million tons (11,625,000 barrels) and by 1958 only 7 mines and 2 opencast workings remained in operation (the latter were in the process of closing), although the industry still employed 2,850 men. Production had totally ceased by 1963; the last working mine was at Westwood (Tranter, 1979; Hendrie, 1986).

2.5 The Parent Rock

The parent rock, from which paraffin is extracted, is a sedimentary rock containing varying amounts of solid organic material (kerogen) that, when heated to 500° C,

yields hydrocarbons. It is not an oil bearing rock and the shale fields never contain any liquid oil (Cadell, 1925). As described the oil shales occur in Lower Carboniferous strata in the Upper and Lower oil-shale Groups (Cameron & McAdam, 1978). Commercially viable deposits are found in Estonia, the Soviet Union, Manchuria, Brazil, and the United States of America.

In West Lothian oil-shale is found from the Firth of Forth, between Blackness and South Queensferry in the north, through the major producing areas to West Calder and Addiewell in the south (Figure 2.1). The strata of the West Lothian oil-shale fields are covered by superficial deposits of boulder clay, sand and gravel beds, and by extensive beds of peat in the south. The thickness of these deposits varies from a few metres to more than 20 metres thick (Cadell, 1925; Cameron & McAdam, 1978). As a result of post-Carboniferous volcanic action, igneous intrusions have produced sufficient heat to distil kerogen out of the oil-shale seams. This produces small pockets of solid wax and liquid paraffin in cavities and fissures of the oil-shale beds at the boundaries with the intrusions (Cadell, 1925).

2.6 The Main "By Product"

The process of retorting crude oil from oil-bearing shale is destructive and results in a vast amount of waste. On average, every 10 barrels of oil manufactured required the extraction of 8 tons of shale and left 6 tons of burnt shale waste (Hendry, 1925; Bradshaw & Chadwick, 1980). This was left lying around the West Lothian landscape in vast piles, the county's unique red shale bings. Bing is a Scots word meaning pile or heap and has been used from the 16th century; its derivation is from the Old Norse 'bingr': a heap (Robinson, 1985).

2.6.1 The physical scale

It is impossible to live, work or travel through West Lothian without being aware of these massive monuments to industry in the area and their overpowering effect on the landscape. It is even more difficult to convey the sheer size of these bings and the amount of shale they contain to someone who has never seen them. Each ton (1.016 tonnes) of fresh shale mined produced a cubic yard (0.765 m^3) of spent shale after

processing. The through put for Scottish Oils in 1923 was 8,000 tons (8,128 tonnes) of crude oil a week. Thus new spent shale was being added to the bings at a rate of 2,920,000 cubic yards (2,233,800 cu. metres) every year. This is the equivalent of a single bing with a volume almost as great as the Cheops pyramid in Egypt (which is 451 ft [137.465 m] high) (Cadell, 1925).

H.M. Caddell produced a wonderful mental image to convey the size of this vast accumulation of spoil in his 1925 publication "The Rocks of West Lothian".

> *From 1883 to 1923 "...the total quantity of spent shale comes to 116,800,000 cubic yards. This large figure will, no doubt, convey little or no meaning to ordinary readers, but if we imagine the material to be all collected into one vast heap, its size can be more easily appreciated.*
> *Let us suppose some titanic magician could sweep up all the shale bings and place them on an equally titanic carpet, then lift it by the four corners and fly with the bundle to the neighbourhood of Arthur's Seat. To demonstrate to the intellectuals of Edinburgh the bulk of the aerial cargo, he might hover over the New Town, pierce the bag and let the shale stream out, as sand streams through the neck of an hourglass. It would form a cone with sides sloping at 40° and the base would reach from the middle of Charlotte Square to the Melville Monument in St Andrews Square, while the top would rise to a height of 1285 ft above George Street, and would be almost level with the crest of Allermiur on the Pentlands. If this were considered too frightful a piece of vandalism to inflict on Scotia's darling seat, our magician might fly seawards and drop the ashes on the foreshore at Portobello, where they would produce a cone 1½ times as high as the ancient volcano of Arthur's Seat." (Cadell, 1925, p310).*

Since that description was written many of the bings have been added to and others have been destroyed. When production ceased in 1962 there were 27 bings containing over 200 million tons of shale (Scottish Development Department, 1966). The red shale has been used as hard core for roads, footpaths, infill for building sites and briefly as foundation material for houses, until builders discovered that the shale reacted with mortar and cement causing new houses to collapse (Hendrie, 1986). The M8 and M9 motorways are founded on burnt shale.

2.6.2 The visual impact

The 19 remaining bings cover 139 Ha (0.4% of the total land area of the county) and, as already described, are significant landmarks in the low lying and undulating landscape (Figure 2.3). The local hills rarely rise more than 200 m above sea level

and the highest natural feature in the county is the Knock in the Bathgate Hills, at 315m (Sheldon, 1997).

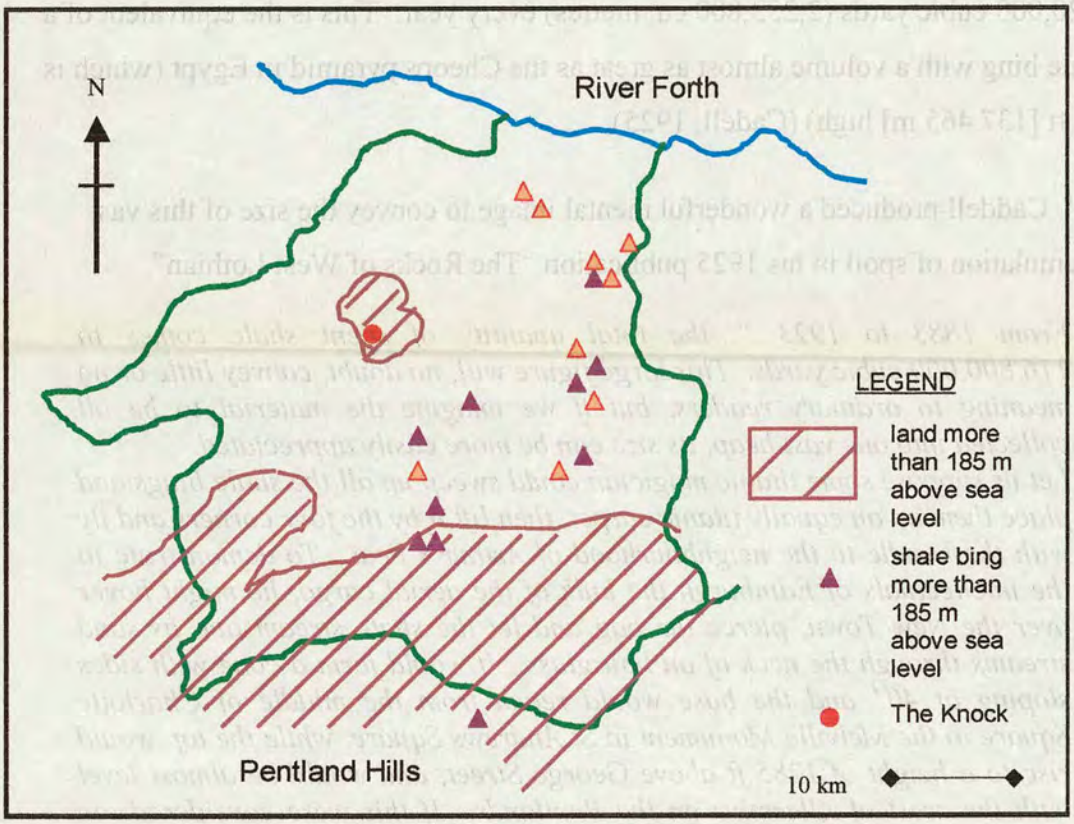


Figure 2.3 Topography of West Lothian

Simplified map of West Lothian displaying all physical features rising more than 185 m above sea level: naturally occurring land as shaded areas and the 10 bings as dark triangles. The Knock, the highest point in West Lothian at 315 m, is displayed as a circle.

The plateaued summit of Greendykes Bing (Figure 2.4) rises to 195 m and towers over the towns of Broxburn and Uphall (Russell, 1971). The multiple peaks of Five Sisters Bing at Westwood (Figure 2.5) resemble the knuckles of a defiantly clenched fist raised above the surrounding agricultural area. This is a landmark so unique that it is reproduced on Newpark roundabout, Livingston (Figure 2.6) and is incorporated into the new West Lothian County logo, alongside the Union Canal and the 39 arch railway viaduct (Figure 2.7).

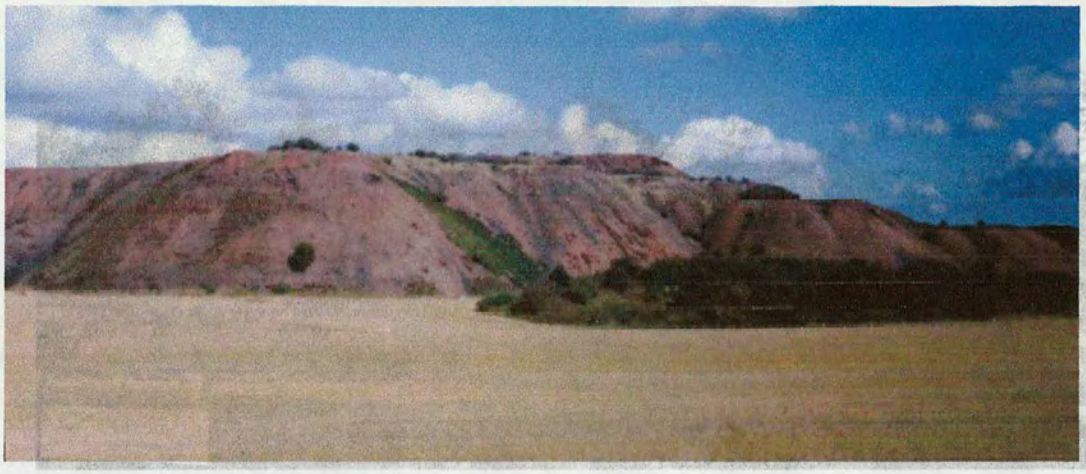


Figure 2.4 Greendykes Bing

Greendykes bing is an Industrial Heritage Site. The most visible of the remaining bings in the county, it is surrounded by agricultural land.

Figure 2.5 Five Sisters

Five Sisters bing (sometimes known as Westfield) is also an Industrial Heritage Site. This bing is unique in having multiple peaks.

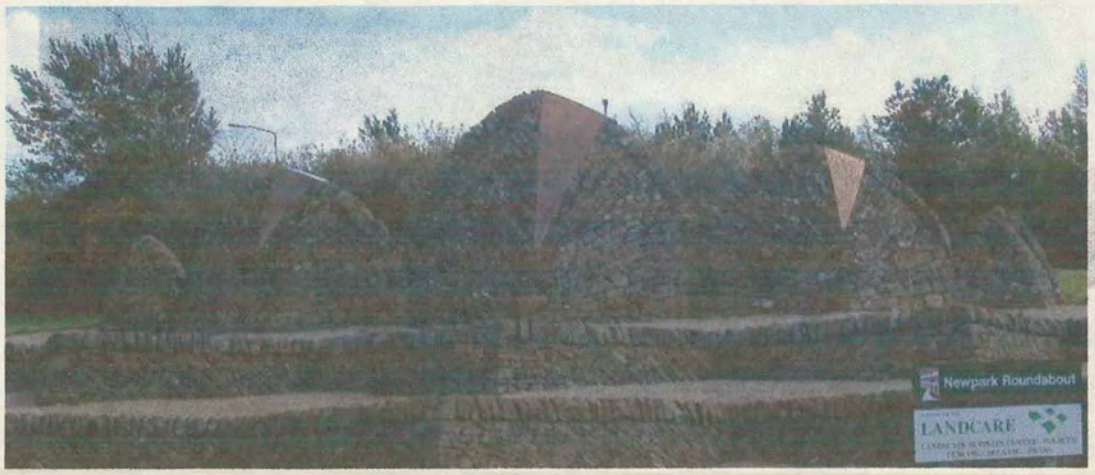


Figure 2.6 Newpark Roundabout

Newpark roundabout, Livingston with its central sculpture replicating Five Sisters in stone and copper.

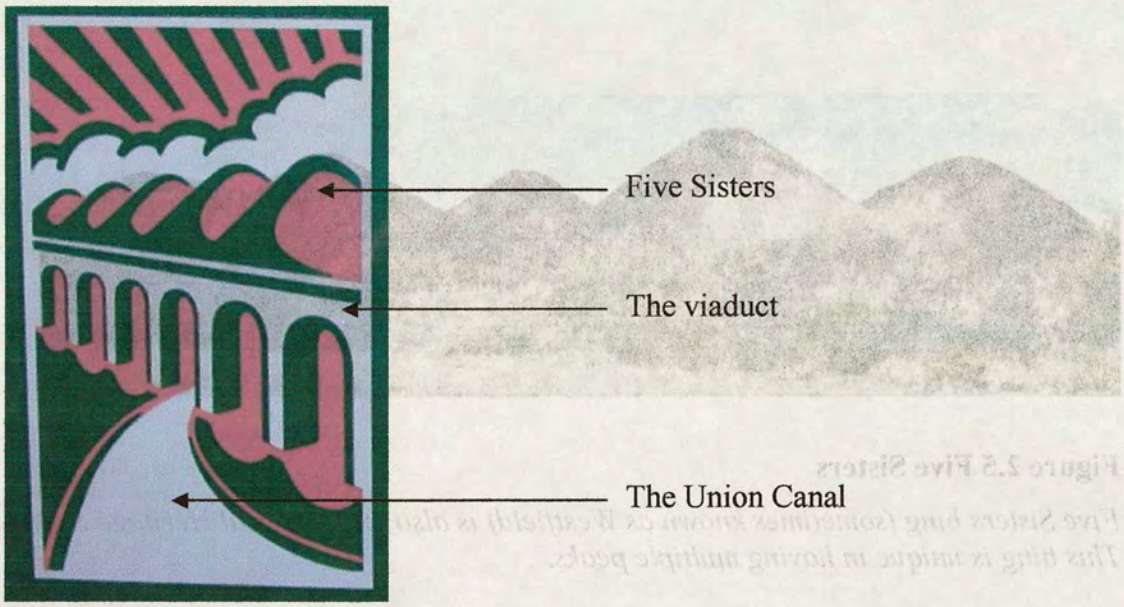


Figure 2.7 West Lothian County Logo

Five Sisters again, this time appearing in stylised form with the viaduct and the Union Canal as part of the West Lothian County logo.

CHAPTER THREE

"Chaos rudis indigestaque moles." (Chaos a rough and unordered mass)

Ovid (43 BC - 8 AD). Metamorphoses, book 4, ch.1, 428.

3 Vegetation Structure on Oil-Shale Bings

The uniqueness and ecological importance of the bings were outlined in Chapter One and these qualities were put into an historical, geographical and geological context in Chapter Two. In order to determine if the processes and mechanisms of vegetation dynamics on the shale bings could be identified using standard ecological methods it was necessary to establish if there was an identifiable structure to the vegetation that could be given an ecological explanation. The initial objectives were to identify any recognisable patterns in the vegetation and to ascertain if the resulting species associations were representative of plant communities recognised elsewhere in Britain by addressing the questions posed in Chapter One, Section 1.8. Subsequent chapters will interpret any patterns with respect to environmental variables and successional processes.

Vegetation and species data from literature on the West Lothian shale bings were collated and re-analysed to determine the completeness and usability of existing information. New data were collected for comparison to test for changes in vegetation over time. A base-line survey was carried out to provide more complete data sets that would be comparable both with existing literature on other habitats and with future surveys, to study long-term environmental and vegetation changes on the bings.

3.1 Vegetation Patterns

There are many examples of vegetation patterns being described and analysed to provide predictive theories of colonisation in a wide range of habitats, both natural and man-made, and the information from these can be compared and contrasted with the structure of vegetation on the bings. In 1986 Grime described "the circumstances

and characteristics of spoil colonization (*sic*)" using data collected in the Sheffield region of northern England and concluded that changes in the vegetation could be predicted from the theory of primary plant strategies (Grime, 1977). These strategies[1] can be allocated to individual species from lists recorded in vegetation surveys of the shale bings, which are also spoil sites, to determine whether competitive, stress tolerant or ruderal species (C, S, and R, the primary strategies) are prevalent in the colonising vegetation. The theories presented in, and data collected for, these publications were combined within a volume describing the patterns of ecological specialisation within angiosperms; a detailed ecological and habitat information for 281 common British species (Grime *et al.*, 1988) that can be used to predict or identify any variation in ecological habitats within and between bing sites.

Cronk and Fuller (1995) presented an overview of a number of the ecological theories of invasion (colonisation). Some of these were general hypotheses with little or no predictive value, for example "disturbance produces gaps that allow colonisation". Others provided predictions of the invasion of species, including "unwanted alien species", in very specific ecological situations that are not readily adapted to other situations or habitats. These theories can, however, provide useful indications of the universal processes and mechanisms of vegetation dynamics that can be related to the potential development of plant communities observed on the shale bings. A more direct comparison of vegetation dynamics and species composition on the shale bings can be made with a description of the ecology of disused pit heaps in England (Hall, 1957) in terms of spoil characteristics, features of the natural vegetation and processes of succession, all of which should be relevant because of the similar geological and industrial histories of the study sites.

The British National Vegetation Classification (NVC) developed by Rodwell (1991a; 1991b; 1992; 1995; 2000) has been used to describe plant communities for surveying

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[1] The word 'strategy' is used when referring to C-S-R functional types throughout the thesis because it is the term used in Grime's 1974 paper when the "vegetation classification by reference to strategies" was first described.

and mapping purposes, in combination with Geographic Information Systems (Gooding *et al.*, 1997). NVC was also used to define the development of abandoned arable land into woodland using records collected over a 100 year period (Harmer *et al.*, 2001), and in the development of a new ecological site classification system for British forests (Wilson *et al.*, 2001). Although both of these examples determine woodland development and description, the same techniques can be used to define and describe plant communities on the bings.

Ellenberg Indicator Values (Ellenberg, 1988)[2] have been applied throughout Europe both to predict habitat conditions from existing vegetation data (Dzwonko, 2001) and to predict the occurrence of vascular plants in a known habitat (Dupré and Diekmann, 1998). Although these have been widely utilised throughout continental Europe the indicator values allocated to individual species are not exactly applicable to the maritime conditions in the British Isles and for this reason Hill, *et al.* (1999) revised Ellenberg's original values for the British flora. The revised values can be used to predict habitat conditions on the shale bings from existing species records.

3.1.1 Data collection

There are several stages involved in collecting, collating and manipulating sufficient relevant data to determine the causes and effects of the various processes resulting in discrete and identifiable plant communities. Sites must be surveyed, vegetation sampled (Tansley and Chipp, 1926; Brown, 1954) and the resulting data classified (Rodwell, 1991a; 1991b; 1992; 1995; 2000), described (Peterken, 1974; Rees and Bergelson, 1997) and analysed (Austin, 1977; ter Braak and Šmilauer, 2002).

3.1.2 Classification and ordination

Classification and ordination are best suited to studies where community structure is the main emphasis. They involve grouping similar entities in clusters, either hierarchically or non-hierarchically. Grime (1974) grouped plant communities by growth strategies in a non-hierarchical ordination; categorising species within a

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[2] This is an English translation from the original German "*Vegetation Mitteleuropas mit den Alpen*" (Ellenberg, 1963)

triangular model describing the balance between competition, stress and disturbance in vegetation (the C-S-R model). The underlying theory behind National Vegetation Classification is also non-hierarchical although the initial divisions are based on large-scale divisions of convenience to enable the manipulation of mire and heath communities, woodland and scrub communities, grassland and montane communities, etc. (Rodwell, 1991a; 1991b; 1992; 1995; 2000). The vegetation classes within each of these divisions are not arranged in any order of rank although sub-division of classes introduces a hierarchy in the later stages of classification. Non-hierarchical systems of defining vegetation are useful for preliminary summarisation of large data sets. They do not analyse relationships in the data but produce composite samples of data that can be subsequently analysed using hierarchical classification.

The most common type of hierarchical classification is the dendrogram that indicates relationships between groups. Central European community classifications split vegetation into ordered ranks (for example Braun-Blanquet 1928; 1964, as cited in Ellenberg 1988). These phytosociological systems are divided into 45 main classes then subdivided into orders, alliances, sub-alliances, associations and increasingly smaller units, thus providing detailed descriptive information of plant cover at a local level. The classifications are used successfully to identify large and small scale patterns of vegetation and plant communities although one disadvantage of this system is the extremely long and complex names of the individual classification types, particularly at association level and below.

3.1.3 Identifying vegetation types

There are several ecological methods of measuring and describing vegetation in terms of community types, autecological attributes of species, functional types and indicator values. I selected four standard texts that are widely used in Great Britain:

1. National Vegetation Classification (NVC), published in five volumes (Rodwell, 1991a; 1991b; 1992; 1995; 2000), is the most used (and abused) vegetation classification system in Britain. This is a classification with standardised descriptions of named and systematically arranged vegetation types, both natural

and artificial, for the whole of Great Britain. In addition to original data for England and Wales, vegetation data were abstracted and collated from published and unpublished sources ranging from classical phytosociological accounts to PhD theses but parts of Scotland, particularly the central belt, are under-represented.

2. The Electronic Comparative Plant Ecology (Hodgson *et al.*, 1995) is a standardised data set containing the biology and ecology of common vascular plants of the British flora as described in Comparative Plant Ecology (Grime *et al.*, 1988). Autecological attributes, including habitat range, soil pH, life history, regenerative strategies and seed dispersal mechanism, are given for 500 plant species. Species with similar traits might be expected to occur within like environments.
3. The C-S-R system (Grime, 1974) is an indicator of the established growth strategy, competitive (C), stress-tolerant (S) or ruderal (R), of the subject species and can be used to identify any predominant traits that vegetation might have. Besides the three primary strategies (C, S and R) there are four secondary strategies (CR, SC, SR and CSR) and twelve tertiary strategy types (e.g. CR/CSR and R/SR) making a total of nineteen functional types in all. C-S-R plant functional types can be allocated to individual species (Hodgson *et al.*, 1999) and published lists are available (Hodgson *et al.*, 1995; Fangmeier, *et al.*, 2003). The functional types allocated to individual species within a community can be combined to produce a single C-S-R signature that will denote the attributes of the vegetation and can be indicative of habitat conditions (Colasanti, 2000). Vegetation description by the C-S-R system is modelled as a triangular ordination or ternary plot (Legg, 2004).
4. In 1963 Heinz Ellenberg (cited in Ellenberg, 1988) allocated a set of ecological indicator values to most European vascular plant species based on their range of tolerance of light, temperature, continentality, moisture, soil pH (reaction), nitrogen, and salt. The indicator values quantify the ecological responses of plants to light (L), moisture (F, from the German Feuchtigkeit), reaction (R, a measure of soil or water pH), nitrogen (N), salt tolerance (S), continentality (K) and temperature (T) compared with other species, based on observed distribution

in field conditions in Central Europe. The original values have been modified to make them more applicable to 1,791 vascular species that grow in the United Kingdom and are presented in "Ellenberg's indicator values for British plants" (Hill *et al.*, 1999). The revised version does not include measures of continentality and temperature because these are not considered to be relevant to the maritime climate of the British Isles. Plant communities can be described in terms of the mean and range of indicator values allocated to individual species and from this the attributes of the physical habitat can be inferred.

Potentially these four sources of information could be used to evaluate existing species data to determine any prevalent physiological traits and resource requirements within a vegetation type. These attributes might indicate processes of invasion, or the range of available habitats, or presuppose the physical and chemical composition of the substrate on the bing sites and can be used to generate hypotheses for further investigation.

3.2 Pre-survey Investigations

To avoid any unnecessary collection of new data as much information as possible was gleaned from material furnished in previous studies of oil-shale bings in West Lothian. These included a plant species list from a mixture of oil-shale and coal sites (Martin, 1992), a plant species list for each of four oil-shale sites (Maka, 1995) and a description of the development of the substrate and a plant species list from three oil-shale sites (Russell, 1971). The primary objective was to decide whether the existing data sets were comparable with each other and compatible with accepted standard classifications and standardised information used for identifying vegetation patterns.

3.2.1 Species identification

A major part of the present work was to identify and record the plant species found within the study areas and relate them to species records from the literature. The more common vascular plants were identified in the field, using a hand lens and Rose (1981) as a guide. Samples of the non-vascular and less common vascular species were collected, and identified in the lab using Clapham *et al.* (1993) and Stace

(1997) for vascular plants and Hubbard (1992) for clarification on some grass species; Smith (1982), Watson (1968) and Dixon (1924) for bryophytes; Purvis *et al.* (1992) and Phillips (1994) for lichens. Species information from older literature references was corroborated using Bentham and Hooker (1937). The dichotomous keys of many British floras are based on the hierarchical taxonomy of species into orders, families and genera (Bentham and Hooker, 1937; Clapham, *et al.*, 1993; Stace, 1997). As the science of Taxonomy has developed, the hierarchy of classification and the names of individual species have been amended to incorporate new information. To counter the resulting variation in nomenclature between different texts and floras the species names adopted by Smith (1982), Purvis *et al.* (1992) and Stace (1997) are followed throughout the thesis.

3.2.2 Results of classification

A compilation of the plant species recorded on bing sites by Martin (1992), Maka (1995) and Russell (1971) listed 297 species of 62 families (Appendix 2). In all three studies the presence of species had been recorded at bing level or as a single list for all sites. There was no information on abundance or distribution of species.

National Vegetation Classification (NVC)

The keys for identifying community types, published in the five NVC volumes (Rodwell, 1991a; 1991b; 1992; 1995; 2000), are designed for use with frequency data from collections of relevés and are not suitable for use with the presence absence data that are available in the existing data sets.

The Electronic Comparative Plant Ecology (ECPE)

The information in ECPE (Hodgson *et al.*, 1995) could not be used effectively with the whole data set of 297 species from existing studies as these were listed simply as present, with no records of abundance or distribution. Fourteen species, however, from 10 families were common to all of the sites described in the studies. These widely dispersed species were compared using ECPE to ascertain if they shared ecological traits that might determine common processes or mechanisms affecting their distribution. Of the 14 species all were perennial and all except *Acer pseudoplatanus* were native. Ten of the 14 species regenerate vegetatively (the

exceptions are *Acer pseudoplatanus*, *Cytisus scoparius*, *Heracleum sphondylium* and *Taraxacum officinale*). All except *Urtica dioica* have strong mycorrhizal associations. In addition the species occupy a wide range of terminal habitats, from waste ground to pasture (as defined by Hodgson *et al.*, 1995), and exploit soils with pH ranging from 4 - 7. Seed dispersal is predominantly by animal or wind and dispersule weights range from less than 0.20 mg to greater than 10 mg in both dispersal categories (Table 3.1).

Table 3.1 The 14 plant species recorded on all sites in the previous studies.

The 14 plant species recorded on all sites described in the MSc and BSc studies (Maka, 1995; Martin, 1992; Russell, 1971) are grouped by family; most common terminal habitat, soil pH, agency of dispersal and dispersule weight as described by Hodgson et al.*(1995)are also listed.*

Habitat key: is reproduced in full in Appendix 3 and referred to in subsequent tables in this chapter.

Soil pH key: The numeral indicates the modal pH class for the species followed by a letter indicating the number of pH classes in which the frequency of the species exceeds 50% of that in its modal class. Thus 5a indicates that the species is most frequent within the range 5-5.9 and has a range of only 1 pH unit. In contrast 4d indicates a mode within the interval pH 4-4.9 and a range of 4 pH units.

Agency of dispersal key: is reproduced in full in Appendix 3 and referred to in subsequent tables in this chapter.

Dispersule (Disp.) weight key: 1 ≤ 0.20mg; 2 = 0.21-0.50mg; 3 = 0.51-1.00mg; 4 = 1.01-2.00mg; 5 = 2.01-10.00mg; 6 > 10.00mg.

Species	Family	Habitat	Soil pH	Agency of dispersal	Disp. weight
Acer pseudoplatanus	Aceraceae	WOODl	7e	WINDw	6
Heracleum sphondylium	Apiaceae	WASTEl	5c	WINDw	5
Bellis perennis	Asteraceae	MEADOW	7c	UNSP	1
Hieracium pilosella	Asteraceae	PASTl	7c	WINDp	1
Taraxacum offinale (agg.)	Asteraceae	MEADOW	7b	WINDp	3
Tussilago farfara	Asteraceae	QRYl	7b	WINDp	2
Cytisus scoparius	Fabaceae	RD/RLY	4c	ANIMe	5
Trifolium repens	Fabaceae	PASTe	5c	ANIMa	3
Chamerion angustifolium	Onagraceae	CINDER	4d	WINDp	1
Plantago lanceolata	Plantaginaceae	MEADOW	7c	ANIMm	4
Holcus lanatus	Poaceae	PASTe	5c	UNSP	2
Rosa canina (agg.)	Rosaceae	HEDGE	7b	ANIMi	6
Salix caprea	Salicaceae	SCRUB	5a	WINDp	1
Urtica dioica	Urticaceae	SOIL	6c	ANIMa	1

C-S-R Strategy

A single C-S-R signature (Figure 3.1) was calculated for the list of 297 species using the C-S-R plant functional types for individual species (Hodgson *et al.*, 1999) described in section 3.1.4.

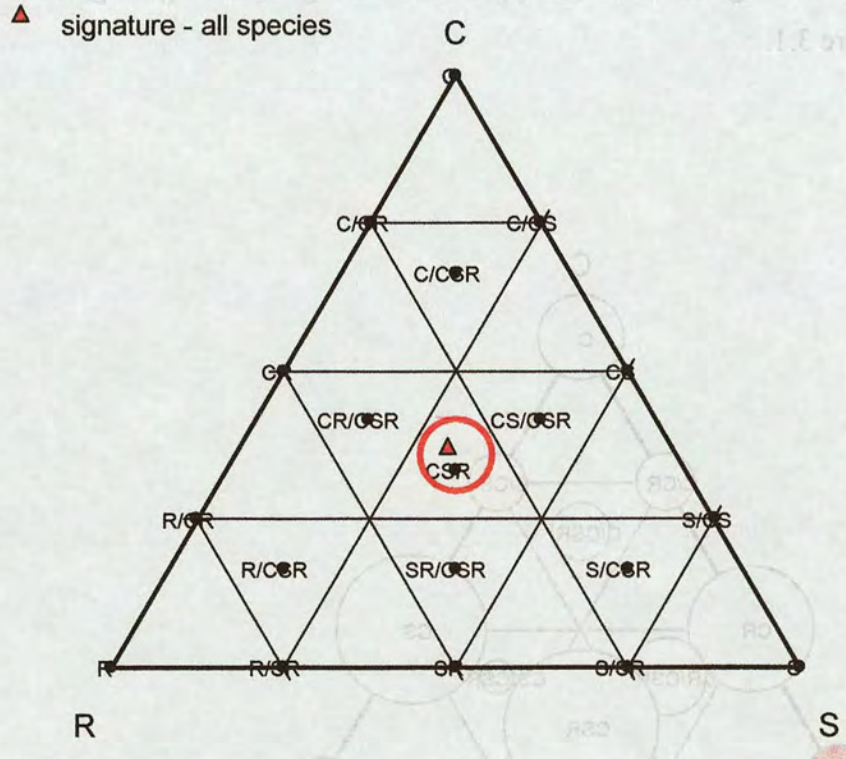


Figure 3.1 The C-S-R signature of the pre-survey vegetation.

The calculated C-S-R signature of pre-survey vegetation (circled) displayed in relation to the 19 C-S-R plant functional types (Grime, 1974).

The resulting signature corresponded closely with the CSR functional type, indicating that either there was no predominance of species allocated to any one of the main functional types (C, S or R) or that there were representative species from all of the functional types. The calculation of a signature does not contribute any information about potential vegetation patterns, as each recorded species contributes equally to the outcome, and it is effectively a mean for all recorded species. The

signature does however provide a benchmark within the C-S-R system of ordination for comparison with C-S-R signatures calculated from species data recorded on individual bing sites or areas within sites and can be used to determine if there is a general shift in species composition towards a functional type which would suggest inter- or intra-site variation in environmental factors. A more complex method of displaying the relative numbers of species allocated to each of different functional types in the C-S-R system as different sized "bubbles" within the triangle (Figure 3.2) demonstrates the range of functional types contributing to the single signature displayed in Figure 3.1.

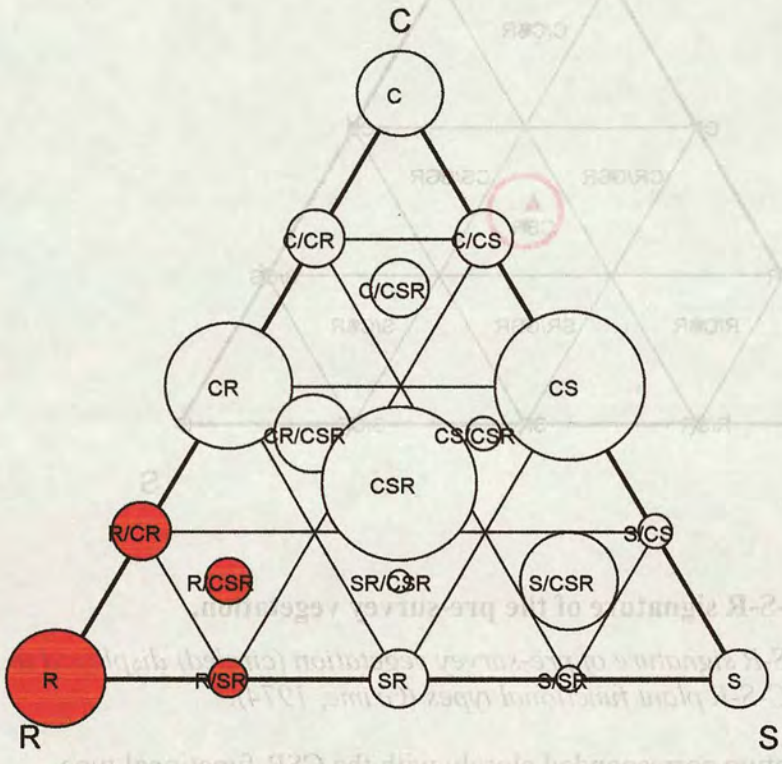


Figure 3.2 The spread of C-S-R types within the signature

The percentage of species allocated to each of the 19 C-S-R plant functional types (Grime, 1974) are displayed as bubbles drawn to scale on the triangular graph. The group of shaded bubbles at the bottom left represent ruderal functional types, 18% (53) of the 297 species.

Ellenberg's Indicator Values

The species recorded in previous studies (Maka, 1995; Martin, 1992; Russell, 1971) were ranked according to the revised Ellenberg Indicator Values for British plants (Hill *et al.*, 1999) allocated to each species (Figure 3.3). Seventeen of the 297 recorded species have no designated values however these are either non-vascular or non-native (introduced) species. Species were ranked separately for light (L), nitrogen (N), moisture (F) and reaction (R) as described in section 3.1.4 and Figure 3.3. This information was used to infer the habitat conditions likely to be found on the bings. The resulting graphs showed that recorded species were predominantly indicative of high light, high pH, and low moisture habitats and that they imply considerable variation in nitrogen availability either within or between bing sites.

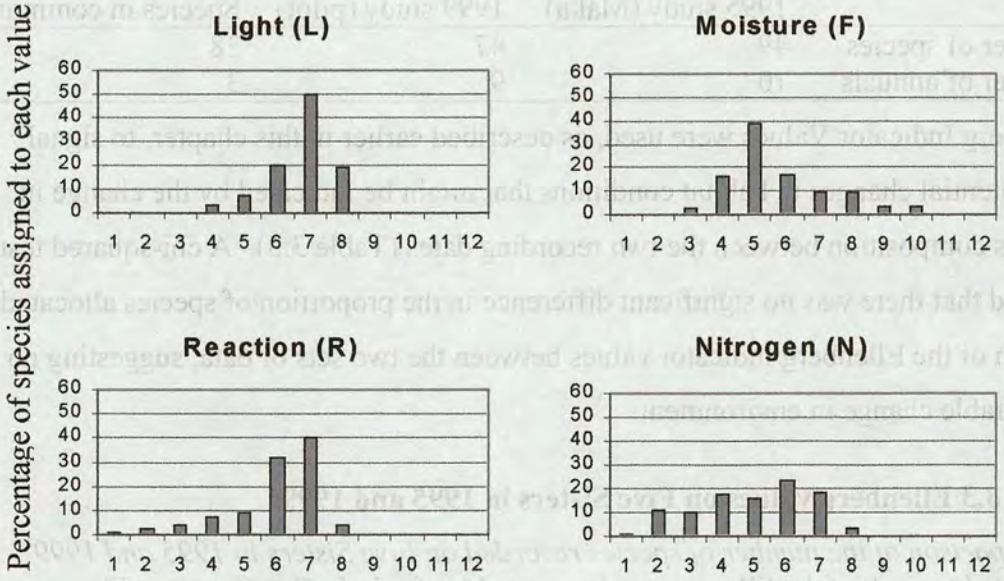


Figure 3.3 Ellenberg Indicator Values for the pre-survey vegetation.

The percentage of recorded species assigned to each value within the range of Ellenberg Indicator Values (Hill et al., *1999) are compared. L (light) ranging from 1 (plant in deep shade - none in UK) to 9 (plant in full light). N (nitrogen) is a general indicator of soil fertility ranging from 1 (extremely infertile) to 9 (extremely rich). F (moisture) ranging from 1 (indicator of extreme dryness) to 12 (submerged plant). R (reaction) measured as soil or water pH ranging from 1 (indicator of extreme acidity) to 9 (indicator of base reaction).*

3.2.3 Pilot study

In order to gauge the rate of succession and any change in the vegetation composition since the original studies on the bings a brief pilot study was carried out on Five Sisters in March 1999. The presence of each plant species was recorded as it was encountered during a single 2-3 hour visit (Appendix 4) to formulate a list that was comparable with the records from Maka's 1995 study of Five Sisters (Table 3.2). The number of vascular species and proportion of annual species in the two studies was almost identical despite the lists having only 28 species in common.

Table 3.2 Species recorded on Five Sisters in 1995 and 1999

The total number of vascular plant species recorded on Five Sisters in 1995(Maka) and in 1999 (pilot study), and the number of annuals recorded in each study.

	1995 study (Maka)	1999 study (pilot)	Species in common
Number of species	49	47	28
Number of annuals	10	9	3

Ellenberg Indicator Values were used, as described earlier in this chapter, to signal any potential changes in habitat conditions that might be indicated by the change in species composition between the two recording dates (Table 3.3). A chi-squared test showed that there was no significant difference in the proportion of species allocated to each of the Ellenberg indicator values between the two sets of data, suggesting no measurable change in environment.

Table 3.3 Ellenberg values on Five Sisters in 1995 and 1999

A comparison of the number of species recorded on Five Sisters in 1995 and 1999 allocated to each of the Ellenberg indicator values for light (L), moisture (F), reaction (R) and nitrogen (N).

Indicator value	L 1995	L 1999	F 1995	F 1999	R 1995	R 1999	N 1995	N 1999
1	0	0	0	0	0	0	0	0
2	0	0	0	0	0	0	2	2
3	0	0	0	0	0	0	2	1
4	1	0	8	5	1	1	13	12
5	0	2	25	29	3	3	7	7
6	6	9	11	11	23	25	18	15
7	32	26	3	1	19	17	5	8
8	9	10	1	1	2	1	1	2
>8	0	0	0	0	0	0	0	0

3.2.4 Discussion of findings

Existing data for plant species on the bings was not sufficient for comparison with NVC.

The characteristics, generated from ECPE (Hodgson *et al.*, 1995), of the 14 species that were common to all of the sites described in the previous studies (Table 3.1) conformed to those expected from literature for early stages of primary succession (Cronk and Fuller 1995). Other characteristics expected in invasive species are high seed production and early reproductive maturity (Cronk and Fuller, 1995). These are traits that are not described in ECPE as they are relative measurements that can vary considerably both inter- and intra- specifically. Significant new data would need to be collected from the West Lothian sites to comment on these species characteristics. The proportion of wind dispersed species in the bing data was higher than expected from the species recorded in vegetation surveys of spoil in the Sheffield area (Grime, 1986) but the topography of the Sheffield sites is not described. Cronk and Fuller (1995) suggest that dispersal of species by wind will be the most efficient mechanism in open ground and on sites that are elevated above the surrounding area, such as bings. They particularly propose that members of Asteraceae are the most likely invaders because of their high seed production. More quantitative information on the frequency and abundance of individual species is needed as the higher number of wind dispersed species on the bings could also reflect a predominance of these species in the surrounding area.

The co-ordinates of the C-S-R signature for the species recorded in the bing vegetation as a whole were very close to those for the CSR strategy (Figure 3.1). This demonstrated that species of no single functional type prevailed on the sites, unless they were all CSR generalists. Convention would expect there to be higher proportions of short lived, high fecundity species (R-strategists) and species best-suited to low-nutrient/water availability (S-strategists) in the early stages of primary succession (Grime, 1977; Harper, 1977). The spread of C-S-R types within the signature (Figure 3.2) demonstrates that a large proportion of the species recorded are allocated to intermediate functional types, CSR, CR and CS, and that only 18%

are ruderal (R) species. This information has to be treated with caution however as each species recorded contributed equally to the calculation of the signature because no measure of abundance of species was available from the existing data. Any variation in the composition of species present within or between individual bings and their different functional types will also have been lost in the bulking of information. Qualitative species abundance data from each bing site should be collected and analysed separately to obtain a better insight into vegetation patterns and succession processes.

The classification of the existing data by Ellenberg Indicator Values (Figure 3.3) demonstrated that species presence alone may be used to generate hypotheses on the expected general habitat conditions likely to be found on the bings. More than 50% of the recorded species were indicative of high light, high pH, low moisture or a combination of these. From this the bing habitat is expected to be open ground with a free-draining, alkaline substrate. These postulates will have to be corroborated by collecting the relevant data so that any variation in substrate chemistry can be related to vegetation patterns.

The pilot study showed that there was little difference in the number of species recorded on Five Sisters between the 1995 study (Maka) and 1999 visit (Table 3.2) although the species lists on the two occasions varied considerably; only 28 species were recorded in both studies (Table 3.2). Despite this when the two lists of species were classified by Ellenberg indicator values there was no significant difference between the number of species allocated to each of the four environmental criteria; light, moisture, reaction and nitrogen (Table 3.3). This indicated that only limited, short-term change should be expected in both nutrient availability and overall vegetation structure and that there was unlikely to be any advantage in frequent (e.g. annual) surveys.

The information derived from the classification of data available from the studies of Maka (1995), Martin (1992) and Russell (1971) provided a broad outline of the range of plant species and nutrient availability that can be expected between and within shale bings in West Lothian. The ecological attributes for those plant species

(Hodgson *et al.*, 1995) and their optimum resource requirements for light, moisture, pH, nitrogen and salt (Hill *et al.*, 1999) provided strong indications of the potential differences in the nutrient status of the substrate within the bing environment. Existing material was not sufficiently detailed to link species, or groups of species, with particular habitat conditions. Significant amounts of new quantitative data on the frequency and abundance of all species were required, as were data on the availability of soil nutrients.

The decision was made that a baseline survey and full description of the bing sites was necessary. Information had to be collected relative to individual bing site and position on that site (e.g. altitude, aspect) to allow analysis of data within and between sites. This would also allow more complete comparisons to be made with data in the literature on other primary succession sites. There was unlikely to be any advantage in replicating the surveys during the current period of study and monitoring the sites every ten or twenty years would probably be sufficient to record any changes in vegetation structure. Different stages of colonisation, including shifts in vegetation patterns or structure of substrate, should be inferable from the changes relating to variations in age, management and size of the individual bings. The new data generated could test the hypothesis that the range of variation in ECPE, C-S-R and Ellenberg grouping of the existing species data can be explained by spatial variability in species associations within and between the bings.

3.3 The Baseline Survey Methods

In preparation for the baseline survey the ownership of individual bings was ascertained and permission to work on them was sought. There are 19 shale bings in West Lothian (Table 3.4 and Figure 3.4). The bings vary considerably in size, shape and age, and in the extent and type of management that has been carried out on them (see Appendix 1 for individual site locations and descriptions).

From the 19 shale bings, eight sites were selected as best suited for the purposes of the investigation (Table 3.4). Permission to use a site for vegetation surveys was the first criterion used in making this selection. The bing sites also had to be physically accessible, representative of a range of size, shape and height and likewise a range of management practices. It was also necessary to make optimum use of those bings where permission for limited experimentation and vegetation manipulation had been authorised.

Table 3.4 The 19 oil-shale bings of West Lothian

The 19 oil-shale bings of West Lothian with standard abbreviation used for each site in this thesis. Sites marked with an asterisk are those selected for investigation in the baseline survey. Individual site locations and full descriptions are detailed in Appendix 1.

Bing Name	abbreviation	Bing name	abbreviation
Addiewell North *	AN	Green Bing	GB
Addiewell South *	AS	Greendykes *	GD
Albyn	A	Mid Breich *	MB
Bridgend	B	Niddry	N
Clapperton *	CL	Oakbank *	OB
Deans	D	Philpstoun North	PN
Drumshoreland North *	DN	Philpstoun South	PS
Drumshoreland South *	DS	Seafield	SF
Faucheldean	FD	Stankards	S
Five Sisters	FS		

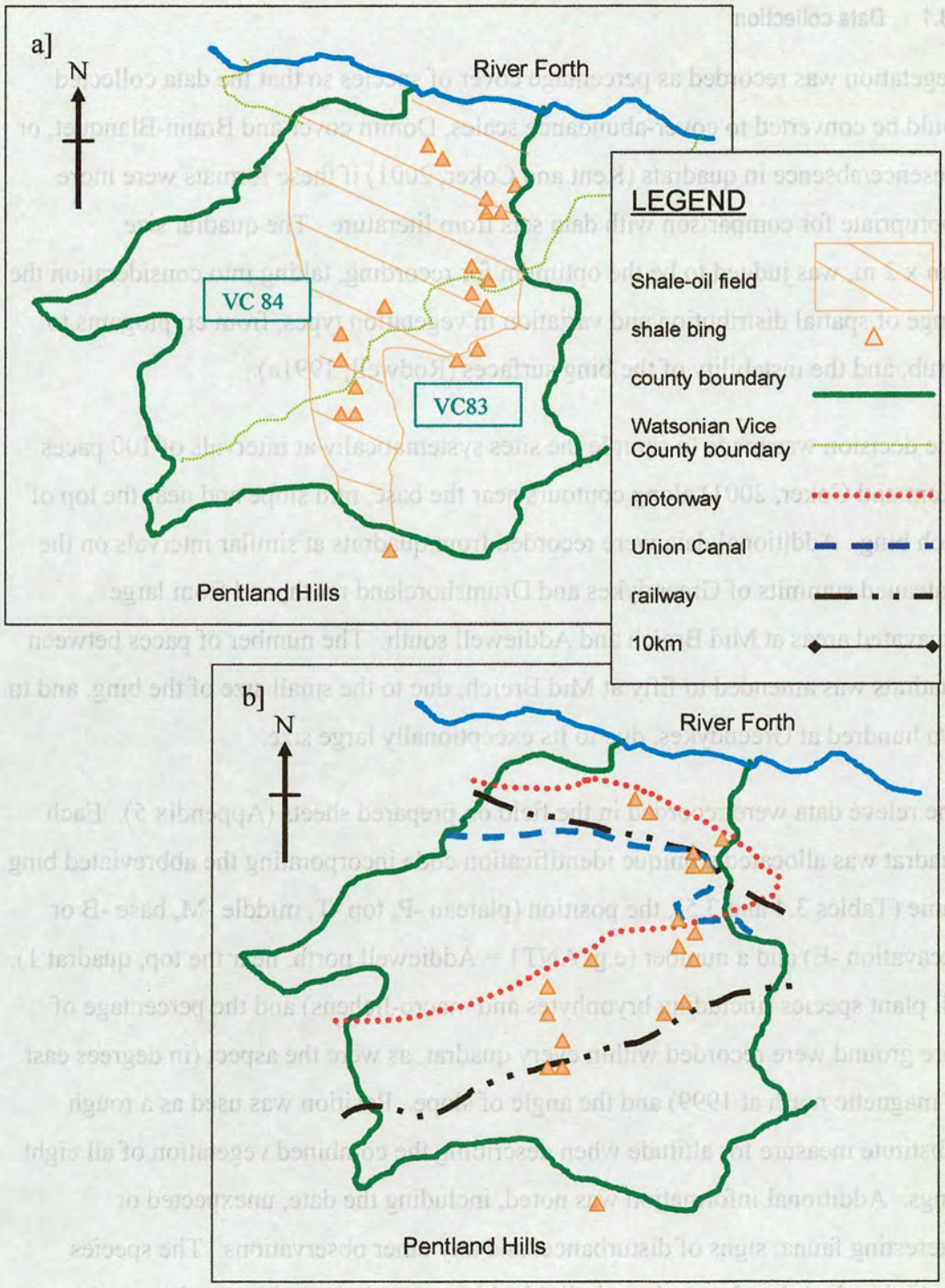


Figure 3.4 Sketch maps of West Lothian.

Sketch maps of West Lothian showing: a) The political boundary, Vice County boundaries, the extent of the shale-oil fields and position of shale bings. b) The main transport routes.

3.3.1 Data collection

Vegetation was recorded as percentage cover of species so that the data collected could be converted to cover-abundance scales, Domin cover and Braun-Blanquet, or presence/absence in quadrats (Kent and Coker, 2001) if these formats were more appropriate for comparison with data sets from literature. The quadrat size, 2 m x 2 m, was judged to be the optimum for recording, taking into consideration the range of spatial distribution and variation in vegetation types, from cryptogams to scrub, and the instability of the bing surfaces (Rodwell, 1991a).

The decision was made to sample the sites systematically at intervals of 100 paces (Kent and Coker, 2001) along contours near the base, mid slope and near the top of each bing. Additional data were recorded from quadrats at similar intervals on the plateaued summits of Greendykes and Drumshoreland north, and from large excavated areas at Mid Breich and Addiewell south. The number of paces between quadrats was amended to fifty at Mid Breich, due to the small size of the bing, and to two hundred at Greendykes, due to its exceptionally large size.

The relevé data were recorded in the field on prepared sheets (Appendix 5). Each quadrat was allocated a unique identification code incorporating the abbreviated bing name (Tables 3.4 and 3.5), the position (plateau -P, top -T, middle -M, base -B or excavation -E) and a number (e.g. ANT1 = Addiewell north, near the top, quadrat 1). All plant species (including bryophytes and macro-lichens) and the percentage of bare ground were recorded within every quadrat, as were the aspect (in degrees east of magnetic north at 1999) and the angle of slope. Position was used as a rough substitute measure for altitude when describing the combined vegetation of all eight bings. Additional information was noted, including the date, unexpected or interesting fauna, signs of disturbance, and any other observations. The species could then be related directly to individual bings, to their position within any bing (henceforth called 'position-on-bing' to differentiate between this and 'position' as a gauge of altitude), or the measured site conditions using data from all bing sites. This would establish if there were variations in patterns of vegetation within and

between bings, and if the patterns were associated with any determined physical environmental factor.

The baseline survey collected data from 340 quadrats on eight bing sites. There were 211 plant species recorded, including bryophytes and macro-lichens (Appendix 6). A breakdown of the survey sites and number of species recorded on each bing can be seen in Table 3.5. Data from 10 or more quadrats were recorded from every position at each site. The exceptions were Mid Breich, where only five quadrats were recorded from the top position due to a combination of dangerous terrain and small site size, and Greendykes, where no quadrats were recorded from the middle position due to lack of time at the end of the growing season. The number of species recorded on each bing site was higher than had been recorded during the pilot study of Five Sisters (Section 3.2.2, Table 3.2) and the species recorded on Addiewell south numbered 104 compared to 81 recorded by Maka (1995), the only comparable data set from the previous studies.

Table 3.5 The number of quadrats sampled at each location

The number of quadrats sampled at each bing site and position-on-site, and the number of plant species, including cryptogams, recorded on each bing site in the baseline survey.

P = plateau, T = top, M = middle, B = base and E = excavated area.

Bing Site	Total quadrats	Number of quadrats at each position-on-site					Number of plant species recorded
		P	T	M	B	E	
Addiewell north (AN)	39	-	16	11	12	-	103
Addiewell south (AS)	54	-	17	17	10	10	104
Clapperton (CL)	53	-	11	20	22	-	93
Drumshoreland north (DN)	40	10	10	10	10	-	60
Drumshoreland south (DS)	11	-	-	-	11	-	49
Greendykes (GD)	70	20	25	-	25	-	86
Mid Breich (MB)	40	-	5	10	15	10	95
Oakbank (OB)	33	-	13	10	10	-	93

3.4 Classification, Ordination and Analysis

Species frequency was calculated as the percentage of quadrats containing each species as used by Grime (1986) and described by Brown (1954). Species affiliation, a measure of grouping patterns within a species, was calculated as mean cover where

present (MCWP), the sum of percentage cover in every quadrat divided by the number of quadrats in which the species was recorded. Species richness was calculated at four levels: total number of species for all sites, combined number of species by bing site, combined number of species by position (plateau, top, middle, *etc.*) and number of species by position-on-site.

The species were grouped and classified using C-S-R strategies (Grime, 1974), Electronic Comparative Plant Ecology (Hodgson *et al.*, 1995) and Ellenberg Values (Hill *et al.*, 1999) as described in the pre-survey investigations (Section 3.1.4). Comparisons were made between and within the data sets using the autecological information. The floristic data were then coded into the computer program ComKey version 0.22 (Legg, unpublished). This software matches species names with the species list used in the VESPAN packages and MATCH program published by the University of Lancaster, Unit of Vegetation Science (Malloch, 1995; 1997). The ComKey program was used for comparing every relevé (floristic data) with National Vegetation Classification (NVC) communities. A variety of weighting methods is available in ComKey that allows the shorter total species lists recorded in single relevés to be compared with NVC type communities. The entire data set was manipulated by site, aspect, position and slope, and various combinations of these, to ascertain the presence of any recurring vegetation patterns within and between bing sites.

3.4.1 General findings

Sixteen vascular species (Table. 3.6), and the moss *Hypnum cupressiforme,* out of the 211 species, were recorded on all eight of the bing sites. Of the vascular plants only two species were also found over the full range of angle of slope (0-80°), position (top, middle, base, excavation and plateau) and full range of aspect (1-360 degrees east from magnetic north), and the full range of percentage bare ground (0-99.99%). These were *Holcus lanatus* (182 quadrats) and *Senecio jacobea* (77 quadrats). *Rumex crispus* (20 quadrats) and *Rubus fruticosus* (16 quadrats) were also in the group of species found at all sites, despite having limited ranges in the environmental gradients. According to Hodgson *et al.* (1995), all sixteen species are

native and perennial. Vegetative regeneration is the main system of expansion in thirteen of the sixteen species (the exceptions are *Dactylis glomerata*, *Cirsium vulgare* and *Taraxacum officinale*). All species except *Urtica dioica* form mycorrhizal associations. The 16 species recorded on all bing sites in the base-line survey occupy a wide range of habitats, seed dispersal is predominantly by animal or wind and there were varying times and durations of flowering. The species are, however, associated with a slightly wider range of soil pH (from 4-7) and a slightly lower range of seed weights, from less than 0.20 mg - 10.00 mg (1-5), in both main dispersal categories (Table 3.6) than the pre-survey species (Table 3.1).

Table 3.6 The 16 vascular plants recorded on all bing sites.

The 16 vascular species recorded on all eight bing sites are grouped by family; most common terminal habitat, soil pH, agency of dispersal and seed (dispersule) weight are also listed (Hodgson et al., *1995). Species also recorded on all pre-survey sites are highlighted with an asterisk (*)*

Refer to the legend of Table 3.1, in section 3.2.1 for Habitat key, Soil pH key, Agency of dispersal key and Dispersule (Disp.) weight key.

Species	Family	Habitat	Soil pH	Agency of dispersal	Disp. weight
Centaurea nigra	Asteraceae	WASTEl	7c	UNSP	5
Cirsium arvense	Asteraceae	COAL	5c	WINDp	4
Cirsium vulgare	Asteraceae	PASTl	5c	WINDp	5
Senecio jacobaea	Asteraceae	QRYl	7a	WINDp	1
Taraxacum officinale agg. *	Asteraceae	MEADOW	7b	WINDp	3
Tussilago farfara *	Asteraceae	QRYl	7b	WINDp	2
Trifolium repens *	Fabaceae	PASTe	5c	ANIMa	3
Epilobium montanum	Onagraceae	QRYl	7c	WINDp	1
Arrhenatherum elatius	Poaceae	SCREE	7c	ANIMa	5
Dactylis glomerata	Poaceae	MEADOW	7c	UNSPag	3
Holcus lanatus *	Poaceae	PASTe	5c	UNSP	2
Rumex crispus	Polygonaceae	CINDER	6b	UNSP	4
Ranunculus repens	Ranunculaceae	MEADOW	6c	AQ/AN	5
Rubus fruticosus	Rosaceae	HEDGE	4b	ANIMi	5
Salix caprea *	Salicaceae	SCRUB	5a	WINDp	1
Urtica dioica *	Urticaceae	SOIL	6c	ANIMa	1

The baseline survey list of species present on all eight bings shared many autecological features with the pre-survey list (Table 3.1). All species were perennials, they were all native (except *Acer pseudoplatanus*), all formed

mycorrhizal associations (except *Urtica dioica*), the main seed distribution agencies were animal and wind, and most of the species regenerated vegetatively. Despite these similarities, only six of the 16 species recorded were common to both lists (Table 3.6).

3.4.2 Species frequency, affiliation and richness

To investigate the distribution and abundance of species in more detail their frequency and affiliation on the shale bings were compared. The species recorded were sorted according to their presence as a percentage of all quadrats (frequency) and the top twenty vascular species were listed (Table 3.7). Their affiliation, measured as mean cover where present, was also recorded. This information was comparable with a study of the flora of spoil habitats in Sheffield by Grime (1986). Two cryptogams, *Hypnum cupressiforme* and *Lophocolea cuspidata* also had high frequencies and affiliations but comparative data were not available from the literature.

Of the top thirteen most frequently recorded species, twelve were also recorded either in Grime's list or on all eight bing sites. *Leucanthemum vulgare* however was recorded on only four of the eight bing sites yet had a frequency of over 36%. This species is recorded as widespread and locally abundant in West Lothian (Smith *et al.*, 2002) and is recognised as being quick to colonise bare ground but is reported as being in decline in Scotland due to a loss of suitable habitats (Preston *et al.*, 2002). This suggests that some of the bings may be acting as significant local refuge sites for this species. Seven of the species appear on all three lists (Table 3.7): Three grasses, *Arrhenatherum elatius*, *Holcus lanatus* and *Dactylis glomerata*; three members of the daisy family, *Cirsium arvense*, *Senecio jacobea* and *Tussilago farfara*; and one nitrogen fixer, *Trifolium repens*. All seven species are common or very common throughout West Lothian and have been recorded over a wide range of habitats (Smith *et al.*, 2002). Of the remaining species *Epilobium montanum* was recorded on all eight bing sites, and *Myosotis arvensis* and *Hypochoeris radicata* were recorded on seven sites. *E. montanum* although prevalent in West Lothian is associated with woodland and *M. arvensis* is usually recorded as an arable weed.

H. radicata, in common with *Senecio viscosus* and *Betula pendula*, is closely associated with bing colonisation (Smith *et al.*, 2002; Muscott, 1989).

Table 3.7 The top twenty plants by frequency and affiliation.

The top twenty vascular species recorded in the baseline survey of the bing sites listed by frequency and affiliation. Two cryptogams with high frequencies are also listed.

** (asterisk) denotes species that appear in the list of 20 most common vascular species of spoil habitats in the Sheffield region (Grime, 1986).*

 # (hash) denotes species that were recorded on all eight bing sites.

Species name	Number of quadrats	Frequency	Affiliation (m.c.w.p.)
Holcus lanatus * #	182	53.5	21.1
Chamerion angustifolium *	141	41.5	8.5
Arrhenatherum elatius * #	133	39.1	15.4
Leucanthemum vulgare	124	36.5	8.4
Deschampsia flexuosa *	123	36.2	39.1
Trifolium repens * #	115	33.8	14.1
Cirsium arvense * #	108	31.8	5.6
Plantago lanceolata *	104	30.6	7.6
Ranunculus repens #	89	26.2	8.0
Tussilago farfara * #	89	26.2	6.5
Cerastium fontanum *	84	24.7	2.2
Centaurea nigra #	81	23.8	10.1
Dactylis glomerata * #	79	23.2	9.0
Festuca ovina	79	23.2	15.5
Senecio jacobaea * #	77	22.7	2.7
Senecio viscosus	69	20.3	5.3
Myosotis arvensis	66	19.4	2.4
Betula pendula	63	18.5	7.5
Hypochoeris radicata	61	17.9	3.2
Epilobium montanum #	60	17.7	1.9
Hypnum cupressiforme	102	30.0	24.5
Lophocolea cuspidata	64	18.8	27.1

One species that did not occur on the list of frequently recorded species on the bings despite being recorded on all eight sites was *Taraxacum officinale* which had only 10% frequency (recorded in 34 quadrats) and 2.3% affiliation (m.c.w.p.). This demonstrated that some widely dispersed species were very sparsely distributed over a wide area. In contrast many species recorded rarely, or in a limited number of sites and positions, were found as large associations of individuals. Two examples are

Fragaria vesca, 6% frequency and 20.0% affiliation, and *Polytrichum commune*, 3% frequency and 16.4% affiliation.

At the other end of the frequency scale, of the 211 total species from the baseline survey there were 48 vascular species (23%) recorded in five, or fewer, quadrats. These appeared, mostly singly, however one quadrat contained six rarely recorded species and another contained five (Table 3.8).

Table 3.8 Six rarely recorded species.

Rarely recorded species at the two Addiewell north quadrats (ANB1 and ANB2) are grouped by family; most common terminal habitat, soil pH, agency of dispersal and seed (dispersule) weight are also listed (Hodgson et al., *1995). Asterisks (*) denote the species that were recorded in both quadrats.*

Refer to the legend of Table 3.1, in section 3.2.1 for Habitat key, Soil pH key, Agency of dispersal key and Dispersule (Disp.) weight key.

Species	Family	Habitat	Soil pH	Agency of dispersal	Seed weight
Cirsium palustre	Asteraceae	PASTl	5c	WINDp	4
Carex flacca	Cyperaceae	SCREE	7c	UNSP	2
Carex nigra	Cyperaceae	MIREu	3c	UNSP	3
Succisa pratensis	Dipsacaceae	PASTl	5b	ANIMa	4
Lotus pedunculatus	Fabaceae	MIREu	5b	UNSP	2
Juncus conglomeratus *	Juncaceae	MIREu	5c	ANIMm	1
Juncus effusus	Juncaceae	MIREu	5d	ANIMm	1
Lysimachia vulgaris *	Primulaceae	MIREs	5c	AQUAT	2
Potentilla anserina	Rosaceae	MIREu	6c	UNSP	3

In contrast to the previous species lists (Tables 3.1 and 3.6) six of these nine species were associated with mires, only one species had wind dispersed seeds and none of the species had a seed weight greater than 2.00 mg. This suggested that the habitat around these quadrats was not the same as in other parts of Addiewell north bing or any of the other seven bings. The substrate may be less free draining than expected or still be affected by mine drainage or seepage. Addiewell north is sited alongside Breich Water, a small river, and adjoins Auchenhard Moss, an extensive marshy area, that is likely to be a major source of seed rain on the northern aspect of the bing.

Both of the quadrats containing many, rarely recorded species were from Addiewell north, base (ANB1 and ANB2), which is protected as a nature reserve (Scottish Wildlife Trust Reserve) because of its wide range of habitat types. It is important that the protected status is maintained. If the shale substrate were extracted it could lead to the potential loss of the marshland habitat type, from the overall bing habitat. The loss of a site for *Lysimachia vulgaris* could be even more significant as the species is exceptionally rare throughout West Lothian (Smith *et al.*, 2002), although this example may be a garden escape.

Species richness was measured over the eight bing sites to investigate any variation in the overall species richness between sites. The number of species recorded in a single quadrat ranged from 0 at Greendykes to 29 at Addiewell north. Box plots showed that the median value for all sites was 13 species and individual bings had a median ranging between 10 and 15 species (Figure 3.5).

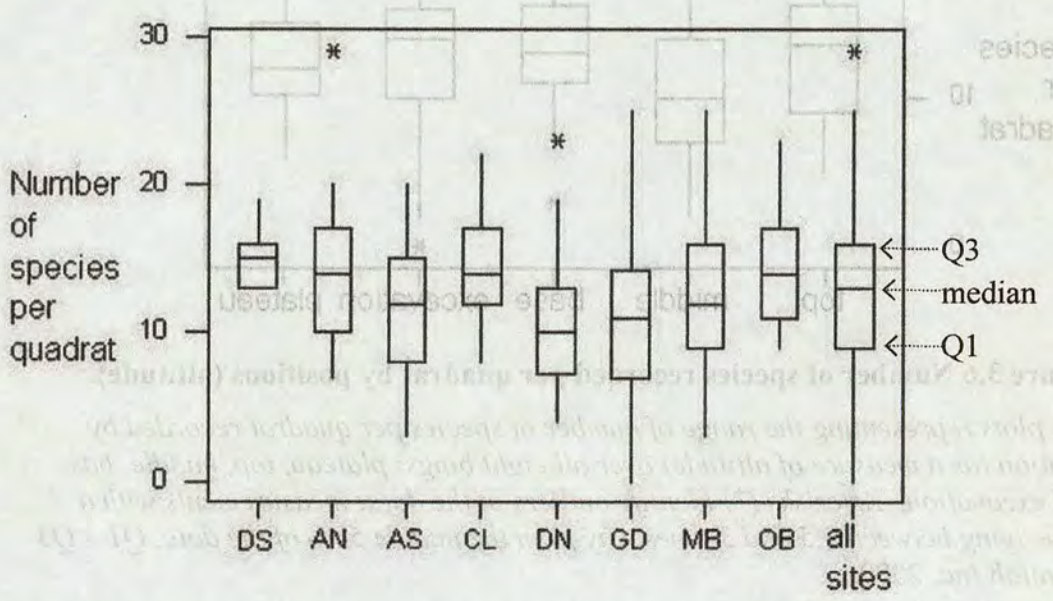


Figure 3.5 Number of species recorded per quadrat on each bing.

Box plots of the number of species recorded per quadrat (2 m x 2 m) in each of the eight bing sites contrasted with a box plot of the species recorded per quadrat in the baseline survey (all sites). DS = Drumshoreland south; AN = Addiewell north; AS = Addiewell south; CL = Clapperton; DN = Drumshoreland north; GD = Greendykes; MB = Mid Breich; OB = Oakbank. Asterisks (*) identify outliers in the data: measurements with a value lying between 1.5 and 3 times way from the middle 50% of the data, Q1 – Q3 (Minitab Inc. 2000).

The extent of inter-quartile variation for all sites pooled was from 9 species (Q1) to 16 species (Q2) with no individual bing site having an inter-quartile range greater than 7.5. The least inter-quartile variation of 3 was recorded at Drumshoreland south and the greatest variation of 7.5 was recorded at Mid Breich.

The quadrat data were re-arranged by position (as a measure of altitude) to describe variation in species richness within the bing sites (Figure 3.6). The median (10-14 species) and inter-quartile ranges (7-16 species) were similar to those for bing sites, demonstrating a comparable range of variation in species richness within and between sites.

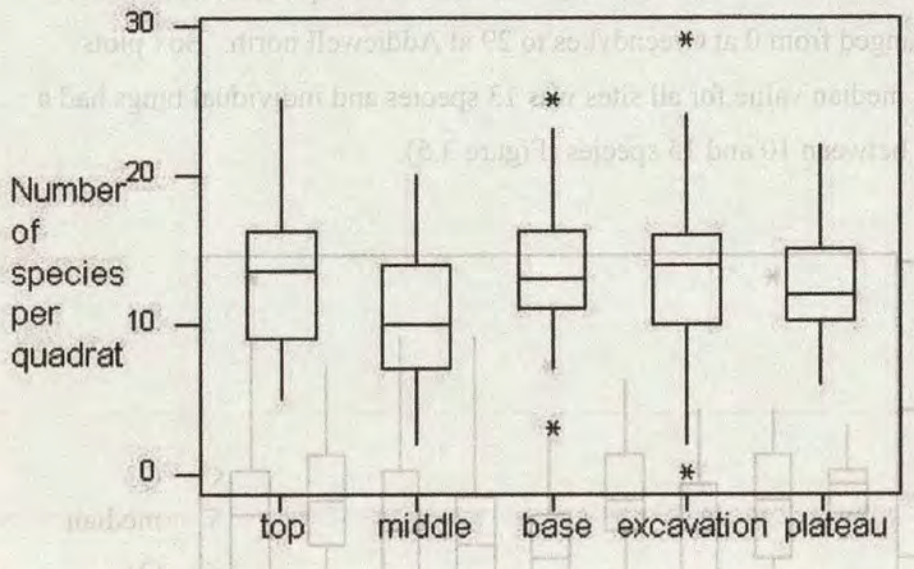


Figure 3.6 Number of species recorded per quadrat by positions (altitude).

Box plots representing the range of number of species per quadrat recorded by position (as a measure of altitude) over all eight bings: plateau, top, middle, base and excavation. Asterisks (*) identify outliers in the data: measurements with a value lying between 1.5 and 3 times way from the middle 50% of the data, Q1 – Q3 (Minitab Inc. 2000).

Finally the quadrat data were ordered by position-on-site to show any smaller scale differences in species richness between and within individual bing sites (Figure 3.7). The positions-on-site with the lowest median of 7 and the highest median of 16.5 were found at the same bing, Addiewell south. There were three positions-on-site with an inter-quartile variation of only three, GDT, DNM and ASB suggesting an evenness of species richness in these areas. The number of species recorded at these

locations varied considerably. ASB had the highest median of all positions-on-site and GDT the third lowest. The greatest inter-quartile variation, of nine, was recorded at MBB suggesting a patchy distribution in species richness.

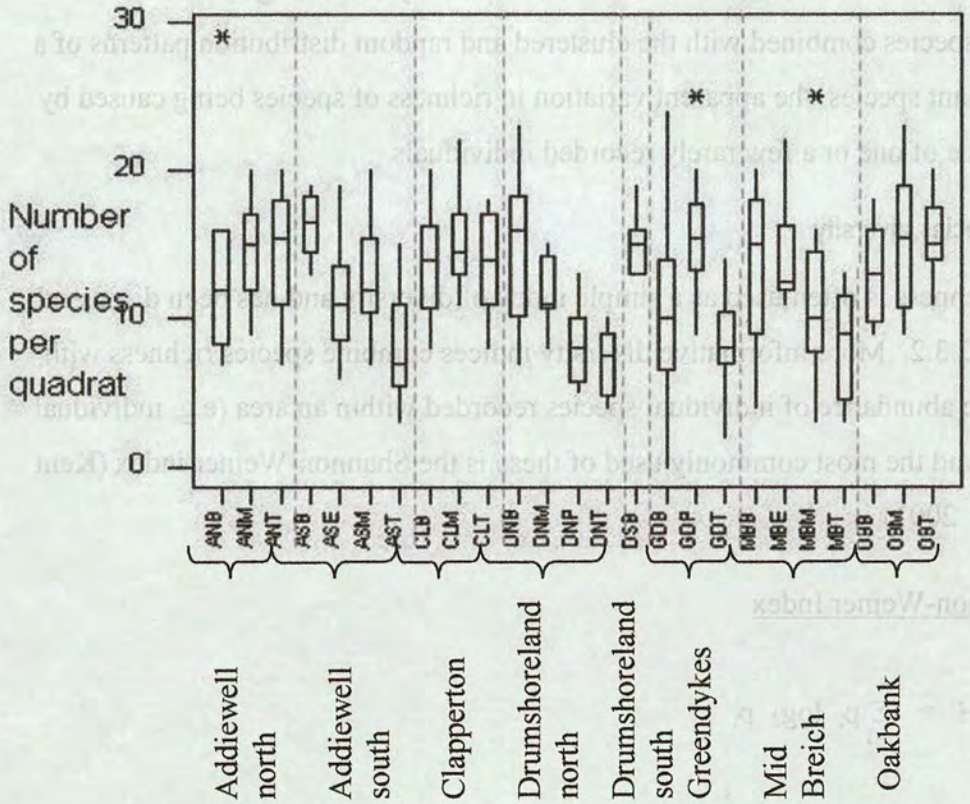


Figure 3.7 Number of species per quadrat recorded by position-on-site.

Box plots representing the range of number of species per quadrat recorded in 25 positions-on-site over the eight bings. Asterisks (*) identify outliers in the data: measurements with a value lying between 1.5 and 3 times way from the middle 50% of the data, Q1 – Q3 (Minitab Inc. 2000).

The greatest overall range of species richness was found at GDB with recordings of 0-24 species over 25 quadrats. This possibly reflects the large size and potentially greater variation in habitat on this vast site (Greendykes bing). The lowest overall ranges were found at ASB, DSB and DNT, with only a six-species margin between the minimum, and maximum recorded values. The number of species recorded differed however, ASB and DSB had between 13 and 19 species per quadrat, and DNT had a minimum of four and maximum of only ten species.

Species richness, measured as the total number of species recorded at a location, varied considerably both between and within bing sites. However frequency and affiliation of species (section 3.3.2) demonstrated that some species were recorded sparsely in a large number of quadrats with many others being recorded in clusters in a few quadrats. This could indicate an overall diversity consisting of widely dispersed species combined with the clustered and random distribution patterns of a few dominant species, the apparent variation in richness of species being caused by the presence of one or a few rarely recorded individuals.

3.4.3 Species diversity

Species richness is often used as a simple index of diversity and has been discussed in section 3.3.2. More informative diversity indices combine species richness with the relative abundance of individual species recorded within an area (e.g. individual quadrats) and the most commonly used of these is the Shannon-Weiner index (Kent and Coker, 2001).

The Shannon-Weiner Index

$$\text{Diversity } H' = -\sum_{i=1}^{s} p_i \log_2 p_i$$

$$\text{Evenness } J = H' / H'_{max} = -\sum_{i=1}^{s} p_i \log_2 p_i / \log_2 s$$

where s = the number of species
p_i = the proportion of individuals or the abundance of the i^{th} species as a proportion of total cover
$\log_2$ = logarithm to the base 2

Values for the diversity index (H') are normally in the range 1.5 to 3.5, although in exceptional cases they can be as high as 4.5. Evenness of species (J) has a maximum value of 1 where all species present have equal abundance. The range of diversity was between 0.50 and 4.31 over the 340 quadrats in the base-line survey. Twenty-nine of the quadrats had indices lower than 1.5 and 19 of the quadrats had indices above 3.5 but the species diversity falls within the normal range of H' in 87% of quadrats. A high diversity index however is not necessarily indicative of a high

evenness score. It is the relationship of both the H' index and J scores with the number of species in the area measured (in this instance the 2 m x 2 m quadrat) that gives information on patterns of species diversity, richness and evenness (Table 3.9 and Appendix 7).

Table 3.9 Examples of Shannon-Weiner indices.

Ten example quadrats selected from the base-line survey. Three with high, 3 with medium and 4 with low species diversity relative to the diversity of the 340 quadrats recorded in the base-line survey. These demonstrate that groups of quadrats with the same or similar Shannon-Weiner diversity indices (H' has a normal range of 1.5-3.5) will have different scores of species evenness (J measured on a scale of 0-1) and number of species recorded (no. of spp.). The Shannon-Weiner indices for all 340 quadrats are in Appendix 7.

	quadrat	H'	J	no.of spp
high	ANB1	4.31	0.90	28
diversity	CLT8	4.17	1.00	18
	GDB2	3.55	0.81	21
'normal'	DNP3	2.98	0.83	13
diversity	CLB9	2.98	0.90	10
	OBT6	2.98	0.71	18
low	AST9	1.30	0.41	9
diversity	CLB5	1.00	0.31	9
	MBB2	1.20	0.76	3
	AST4	0.75	0.47	3

The high diversity group represents the 19 quadrats with a score greater than 3.5 in the diversity index (H'). They demonstrate that although there was a large number of species recorded in each of the three quadrats the species are evenly distributed. They also illustrate how similar results need to be studied carefully. GDB2 had the lowest evenness score of these 19 quadrats (J = 0.81) mainly caused by clumps of *Deschampsia flexuosa*, *Ranunculus repens* and *Chamerion angustifolium* each covering 20% of the quadrat while the remaining 18 species were recorded at between 1% and 5% cover. CLT8 had a perfectly even distribution with all 18 of the species recorded at only ≤1% cover (and 95% bare ground). ANB1 also had an even distribution with 20 of the 28 species recorded at between 5% and 10% cover and no larger clumps of species. The group representing quadrats from the normal range of diversity had the same H' value and shows that when diversity is the same, evenness

is negatively correlated with the number of species recorded. Hence the lowest J value (0.71) corresponds to the highest number of species recorded (18) in OBT6 and the highest J value (0.90) corresponds to the lowest number of species recorded (10) in CLB9. The examples of low diversity indices are two pairs of quadrats, each with the same number of recorded species, that display different H' and J' values. The two quadrats with nine species, AST9 and CLB5, had similar scores for both diversity and evenness. AST9 was dominated by *Deschampsia flexuosa* (80%) with the remaining eight species recorded at 5% cover or more. CLB5 was dominated by *Medicago lupulina* (90%) with the remaining species recorded at 1% cover. The diversity and evenness scores of the quadrats with only three recorded species, MBB2 and AST4, are more dissimilar, particularly the J scores. The relatively high J score for MBB2 demonstrates that the three species were each recorded at ≈5% cover with a high percentage of bare ground in the quadrat (similar to the 'perfect' evenness shown in CLT8, with a high diversity score). Conversely AST4 was dominated by *Deschampsia flexuosa* (90%) and the other two species recorded with only 5% cover.

The Shannon-Weiner Index of diversity and related evenness scores for the individual quadrats reinforced the evidence of variability in the bing vegetation suggested in the previous section (3.4.2 Species frequency, affiliation and richness) and demonstrated the intricacy and variation in the distribution of assemblages of recorded species. This new information could now be integrated with the standard species attributes from literature that were introduced in the pre-survey classifications.

3.4.4 Ordination by ecological indicator values (Ellenberg)

Of the 182 vascular plants recorded in the baseline survey over all bing sites, 34 species have not been allocated Ellenberg indicator values (Hill, *et al.*, 1999). The indicator values for L (light value), F (water value), R (reaction value), and N (nitrogen value) were considered to be the most relevant to the vegetation. The pre-survey classification gave a strong indication that salinity is not a limiting factor on the bings, and K (continentality) and T (temperature) values are not calculated by Hill *et al.* (1999) as they are not considered to be an issue in Britain. The species

were ranked according to their allotted indicator values and the range of values for each indicator were recorded and the results were compared with the pre-survey data (Figure 3.8) to reveal the likely attributes of the bing sites. It is important to note that although R is an indicator of acidic and basic soils the values are not synonymous with pH values.

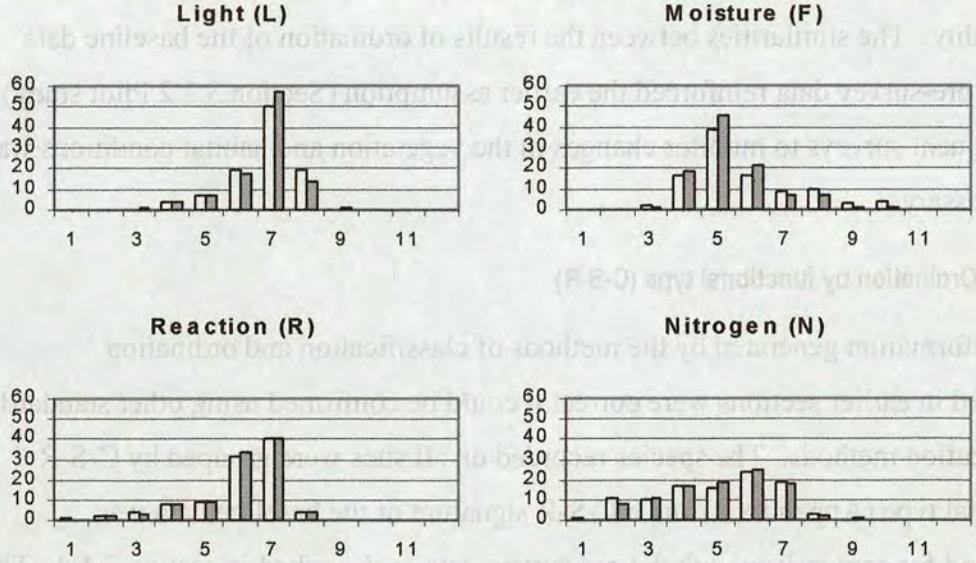


Figure 3.8 The percentage of recorded species assigned to each value within the range of Ellenberg numbers

The percentage of recorded baseline species ■ and pre-survey species □ assigned to each value within the range of Ellenberg Indicator Values (Hill, 1999) are compared. L (light) ranging from 1 (plant in deep shade - none in UK) to 9 (plant in full light). N (nitrogen) is a general indicator of soil fertility ranging from 1 (extremely infertile) to 9 (extremely rich). F (moisture) ranging from 1 (indicator of extreme dryness) to 12 (submerged plant). R (reaction) measured as soil or water pH ranging from 1 (indicator of extreme acidity) to 9 (indicator of basic reaction).

This simple ordination showed clearly that the distribution of species within each of the Ellenberg categories was similar for the baseline and pre-survey records. In both studies a large proportion of the species recorded had high requirements for light and for neutral to basic reaction. Although a few species had requirements for extremely rich soil (N≥8) the remaining species were distributed, almost evenly, between requirements for low and medium nitrogen values. In the baseline survey no species were recorded at high (>8) water values. Moisture values have a broader range than the other indicators therefore values of 7 and 8 are "damp site indicators, mainly on

constantly damp, but not wet, soils" (Ellenberg, 1988). The distinction in moisture range between the baseline and pre-survey records probably reflects the inclusion of coal spoil vegetation in the pre-survey data. Coal spoil is widely recognised as having very poor drainage. Ordination using Ellenberg indicator values produced an overall picture of the baseline survey bing habitats as a high light, neutral to basic environment with moist to free draining soil and considerable variation in nitrogen availability. The similarities between the results of ordination of the baseline data and the pre-survey data reinforced the earlier assumption (Section 3.2.2 Pilot study) that frequent surveys to monitor changes in the vegetation and habitat conditions was not necessary.

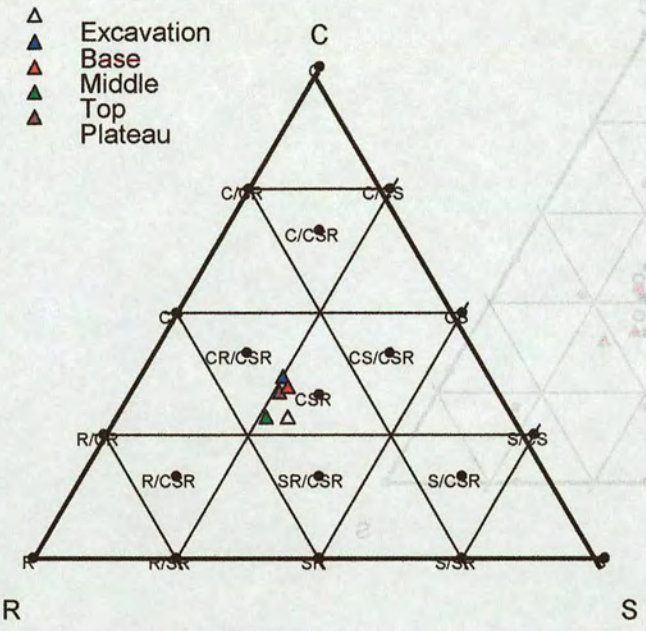
3.4.5 Ordination by functional type (C-S-R)

If the information generated by the methods of classification and ordination described in earlier sections were correct it could be confirmed using other standard classification methods. The species recorded on all sites were grouped by C-S-R functional type (Appendix 8) and a C-S-R signature of the baseline data was calculated for comparison with the pre-survey data as described in section 3.1.4. The species were then grouped according to site, position and position-on-site, and individual C-S-R signatures were calculated for each location. Signatures were also calculated using a list of 1000 common European species (Fangmeier, *et al.*, 2003) and of the 500 common British species described by ECPE (Hodgson *et al.*, 1995) as benchmarks for comparison (Figure 3.9 a, b, c and d).

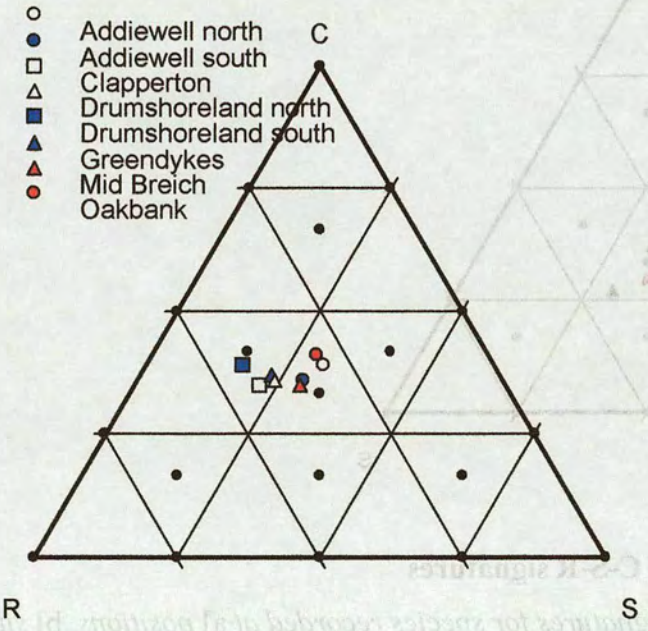
The 'by position' signatures (Figure 3.9 a) are clustered together near the CSR point and within the R:CR:CSR:SR sector of the triangular ordination. The plots approximately follow the CR axis with the base, middle and plateau points closer to C and the top and excavation points closer to R.

The 'by site' signatures (Figure 3.9 b) approximately follow the RS axis. They are less closely grouped than the signatures by position. Five signatures are within the R:CR:CSR:SR sector, the plots run from MB at CSR, via DN, GD and CL, to DS at CR/CSR. Three signatures are within the C:CR:CSR:SC sector, the plots are grouped closely to CSR.

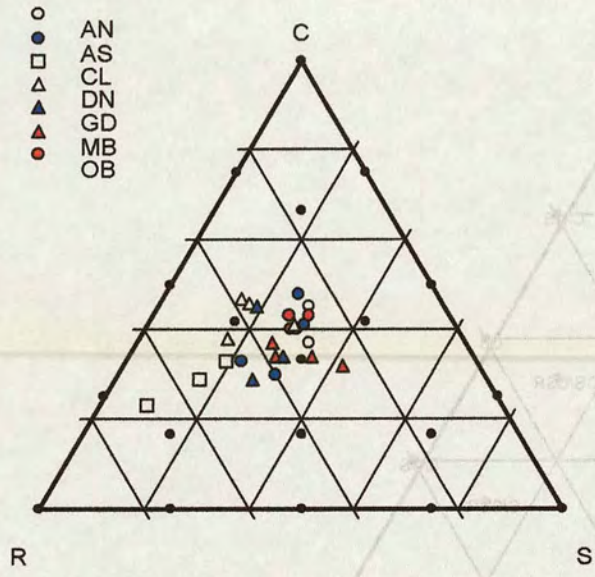
a] signature by position



b] signature by site



c] signature by position-on-site



d] benchmark signatures

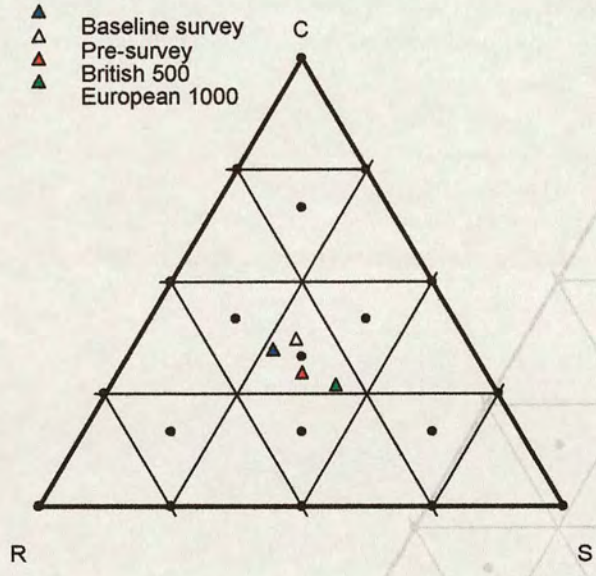


Figure 3.9 Ternary plots of C-S-R signatures

Ternary plots of the C-S-R signatures for species recorded at a] *positions,* b] *sites and* c] *position-on-site demonstrating the variation between and within sites. For comparison* d] *benchmark signatures were calculated using the full baseline and pre-survey species lists, and the published lists of 500 British (Hodgson* et al., *1995) and 1000 European (Fangmeier* et al., *2003) species.*

The 'by position-on-site' signatures (Figure 3.9 c) are less closely grouped than the 'by site' and 'by position' signatures and are spread over a larger area of the graph. There are points in all three sectors. Two plots from MB appear in the S:SC:CSR:SR sector, the only plots that tend towards S. All three CL plots tend strongly toward R and the AN and OB plots tend toward C. The remaining 14 plots are interspersed, with no obvious groupings relating to site or position.

The signatures calculated as benchmarks (Figure 3.9 d) are in all three sectors of the triangle.The signature of the European species lies within the S:SC:CSR:SR sector and the signature of the British species fractionally within the R:CR:CSR:SR sector. The baseline signature is also in this sector but lies toward the CR axis. The pre-survey signature is within the C:CR:CSR:SC sector a similar distance from the British signature but lying toward C.

As with the classifications described earlier in this chapter, the ordination by C-S-R functional type tantalisingly displayed that there was variation in vegetation between and within bing sites but did not produce any definitive divisions. The CL (Clapperton) positions could tentatively be classed as closer to R/CSR than the other positions-on-site (Figure 3.9 c). A series of more complex ternary plots with bubble points is presented in Appendix 9 to demonstrate the variation in functional type within each of the signature points illustrated in Figure 3.9. The implication from the benchmark C-S-R signatures was that common European species tend towards stress tolerant strategies by comparison with common British species, that the baseline signature tended toward CR strategies and the pre-survey signature toward C strategies compared to that for Britain as a whole. The lack of clarification suggested that site, position and position-on-site may be pooling data on too large a spatial scale to identify vegetation patterns in the bing habitat.

3.4.6 Ordination by National Vegetation Classification (NVC)

ComKey (Legg, unpublished) is a computer program designed to compare relevé and community data with NVC communities (Section 3.3. and Appendix 10). The species data from 340 quadrats were matched to their closest NVC communities using three different matching coefficients:

1. Dominance Constancy (DC) - Tests if the most abundant species in the sample have a high constancy in the community. Calculates a mean of the constancy value which is weighted by the ranked abundance of the species. Takes community presence-class into account but not abundance in sample. Suitable for single relevé data (described in Hill, 1989).
2. Hill's G (Hill, 1989) - A weighted combination of compositional satisfaction (CS), dominance satisfaction (DS) and dominance constancy (DC).

   $$0.5* CS + 0.25*DS + 0.25*DC$$

   CS is based on the expectation that 85% of species in presence class V should be present in the sample (described in Hill, 1989).

   DS tests if the sample cover is similar to that of the potential dominants in a community (species with a presence class of III, IV or V and a maximum cover of Domin 5 or upwards). It uses a similarity index based on the expectation that 85% of species in presence class V will be present, 65% of species in presence class IV will be present and so on (described in Hill, 1989)
3. Presence weighted and species match - give weight to species abundance when they appear in both the sample and the NVC community (full descriptions of all coefficients available in ComKey are in Appendix 10).

Dominance constancy and Hill's G were selected as being the most suitable for use with single relevés and incomplete data sets. This was based on their descriptions by Hill (1989). The third (combined) coefficient was considered to be particularly suited to the developing vegetation on the bings because the combination gives weight to the most frequent species and those species with fidelity to a limited number of NVC communities while disregarding species that are missing from the recorded sample. The matches are also suited to single relevé data.

The coefficients classified the 340 quadrats within all NVC vegetation types from swamp (S) to sand dune (SD) and there were obvious disparities in the results caused by the different matching criteria in each of the methods (Table 3.10). It should be reiterated that 2 m x 2 m quadrats, as used in this study, are not the optimum recording size for every type of vegetation. Woodland and scrub is normally recorded on a larger scale (Section 3.3.1 Data collection). However Rodwell (1991a)

elected to use this size for most herbaceous vegetation and heathland when compiling data for NVC, only using larger quadrat sizes when vegetation was taller or more open (the defining criteria of tall and open are not given).

The individual quadrats were matched to a wide range and number of NVC communities within each NVC type and the distribution did not follow the same pattern for each coefficient. There was considerable variation in agreement between the three matching coefficients in allocating quadrats to different communities (Table 3.11). Matching by Dominance Constancy classified the quadrats into 69 NVC communities, by Hill's G classified the quadrats into 70 NVC communities, and by the Combination of weightings classified the quadrats into 53 NVC communities.

Table 3.10 NVC types

The number of individual quadrats allocated to each NVC vegetation type by the three matching coefficient methods; Dominance constancy, Hill's G and the Combination coefficient.

NVC type	Dominance Constancy	Hill's G	Combination
CG (calcicolous grassland)	24	24	22
H (heathland)	92	35	9
M (mire)	5	3	2
MC (maritime cliff)	24	7	1
MG (mesotrophic grassland)	81	146	189
OV(other vegetation)	73	51	62
S (swamp)	0	1	0
SD (sand dune)	3	10	9
U (calcifugous grassland)	21	30	13
W (woodland and scrub)	16	32	32
no vegetation	1	1	1
total no. of quadrats	340	340	340

Table 3.11 Agreement between matching coefficients

Agreement between different matching coefficients in categorising individual quadrats to different NVC communities.

NVC match agreement	no. of quadrats
all three agreed	27
Hill's G + Dominance Constancy	100
Hill's G + Combination	81
Dominance Constancy + Combination	37

Although there was substantial disparity in the matching of individual quadrats to NVC communities, the three different coefficients agreed that most of the plant communities recorded in quadrats from Greendykes plateau and top areas were closest to CG (calcicolous grassland) types. Those recorded from Addiewell north top area were closest to H (heathland) types, those from Greendykes base area were closest to MG (mesotrophic grassland) types and those from all Clapperton areas were mainly closest to OV (other vegetation) types (complete list Appendix 11).

To test these results the quadrat data were grouped by position-on-bing and the species frequencies were matched to their closest NVC community (Table 3.12) using a combined Matched Frequency and Species Match weighting (Appendix 10). This confirmed Greendykes plateau site (GDP) as nearest to NVC calcicolous grassland (CG) types and Clapperton (all sites CLT, CLM and CLB) as nearest to NVC other vegetation (OV) types. The NVC matches for Addiewell north top site (ANT) and for Greendykes base site (GDB) were both woodland (W) types, different from the individual quadrat matches for these positions. The "second best" match was also noted because in many instances despite the scores being similar, or in some cases the same, this was a different type and community from the best match (ANM = MG1 and W9).

There are several possible reasons for the apparent discrepancies between matches. There may be more than one vegetation type present within each position-on-site grouping, as suggested in previous classifications and ordinations. The bing plant communities are probably still developing and therefore represent incomplete species lists for comparison with NVC communities. It is also possible that the vegetation on the oil-shale bings is as unique as the bings themselves and does not comply with the abstract classifications of standardised communities.

In an NVC survey it usual to sample from within a "reasonably homogeneous stand" of vegetation (Rodwell, 1991), then confirm or clarify the community type. The quadrat data collected in the base-line survey were artificially grouped by their similarity to particular named plant communities and these, in many instances, corresponded with particular locations within bing sites. If these sets of quadrats had

been collected in a standard NVC survey then they would be classed as certain communities. There is a danger, however, that emphasis on classifying as a way of describing the vegetation patterns on the bings will result in the loss of awareness of the dynamics of the successional processes by "putting concrete vegetation into abstract boxes" (Legg, 1992)

Table 3.12 The best and next to best NVC community matches

The best NVC community matches for each position-on-site by matched frequency and species match. The second nearest match is also shown for comparison. To demonstrate how close the second matches are to the first, the matched frequency and species match scores are shown with the second match score in brackets. Asterisks (*) highlight matches where the score is the same, or greater (for species match) for the two communities.

The first two letters of the site donate the bing name. AN = Addiewell north; AS = Addiewell south; GD = Greendykes; DN = Drumshoreland north; DS = Drumshoreland south; CL = Clapperton; MB = Mid Breich; OB = Oakbank. The suffix letter donates the position. B = base; M = middle; T = top; P = plateau; E= excavation.

position-on-site	NVC community	second match	matched frequency		species match	
ANB	MG9	MG1	43	(42)	27/53	(24/53)
ANM	MG1	W9	41 *	(41)	30/61	(29/61)
ANT	W9	W11	40	(36)	28/60	(26/60)
ASB	W8	W10	34	(33)	23/52	(22/52)
ASE	SD8	CG2	44	(39)	22/40	(20/40)
ASM	MG1	MG9	41	(35)	30/62	(25/62)
AST	SD8	MG9	49	(48)	26/44	(24/44)
CLB	OV10	OV23	40	(39)	38/81	(37/81)
CLM	OV10	OV19	51	(43)	34/54	(28/54)
CLT	OV10	OV9	54	(49)	29/41	(26/41)
DNB	CG3	SD8	39	(36)	20/41 *	(21/41)
DNM	MG1	OV23	47 *	(47)	21/33 *	(21/33)
DNP	W8	OV9	33	(32)	7/19 *	(8/19)
DNT	MG1	OV23	53 *	(53)	12/17 *	(12/17)
DSB	OV23	MG1	45	(44)	28/49 *	(29/49)
GDB	W24	W8	37 *	(37)	27/59	(26/59)
GDP	CG2	CG4	44	(43)	26/44	(24/44)
GDT	SD7	OV23	47	(41)	22/41	(21/41)
MBB	MG1	SD8	32	(31)	28/73	(26/73)
MBE	CG2	SD8	38 *	(38)	24/50	(23/50)
MBM	U1	SD8	35	(34)	22/52 *	(22/52)
MBT	U20	U1	41	(37)	9/21 *	(10/21)
OBB	W10	W24	41	(28)	28/61	(27/61)
OBM	W10	W8	45	(42)	30/56	(29/56)
OBT	MG1	MG9	47	(45)	28/43	(26/43)

As there was no definitive classification it was decided to determine vegetation patterns and potential communities of species using numerical analysis. Formal analyses of the data were made by two-way indicator species analysis using the TWINSPAN (Hill,1979) routines implemented in PC-ORD version 3.0 for Windows (McCune and Mefford, 1997).

3.4.7 Classification Using Two-Way Indicator Species Analysis

PC-ORD is a formal computer package that, among other things, performs two-way indicator species analysis (henceforth referred to as TWINSPAN[3]) on vegetation data. It does not use environmental information but classifies vegetation by the abundance of species and constancy of occurrence with other species as recorded in individual quadrats. Analysis was set at five levels of division because the majority of groups generated had fewer quadrats than were recorded at any single position-on-site (9 groups represented ≤ 4 quadrats), and further divisions could be based on the presence or absence of individual species. The analysis resulted in 28 groups of quadrats (Appendix 12), a small number in comparison with the number of NVC communities generated (Section 3.4.6). TWINSPAN also allocated the 100 most frequently recorded species into 18 groups from the divisions in the data (Appendix 13). The decision was made to use only these 100 species in the analysis because the main objective was to establish that associations of species recurred to form recognisable patterns in the vegetation. There has been no attempt to reassess the validity of the divisions of TWINSPAN for the same reason.

Several of the TWINSPAN quadrat groupings coincide with individual bing sites (Table 3.13 a). Quadrat groups 01000 and 01001 (both within the 3rd level division 010) contained only quadrats from Greendykes bing (CR/CSR in Figure 3.8 b) and accounted for 31 out of the 70 quadrats recorded for that site. The predominant species in this group were *Euphrasia nemorosa*, *Hypnum cupressiforme* and *Trifolium campestre*. *H. cupressiforme* had already been recognised as being present

[3] Technically TWINSPAN is the name of Hill's (1979) original computer programme. This is re-implemented in PC-ORD. Two-way indicator species analysis is the type of analysis done by TWINSPAN.

on all bing sites but was particularly prolific on Greendykes. *E. nemorosa* (hemiparasite) and *T. campestre* (nitrogen fixer) are both annuals, SR strategists and associated with pH levels of 6 or greater (Hodgson *et al.*, 1995) and with indicator values of R=6 and N=4 (Hill, *et al.*, 1999) suggesting a basic, low nutrient substrate.

Table 3.13 TWINSPAN groupings by site and position

The pattern of quadrats from each bing site a] and position b] allocated to the TWINSPAN groups. Site codes are as defined in Table 3.4. Position codes are as defined in Table 3.5. The first 3 (of 5) levels of division in TWINSPAN are indicated 1^{st} *level* ═══ 2^{nd} *level* ——— 3^{rd} *level* - - - - -

a]

Twinspan group	quadrats by site							
	an	as	cl	dn	ds	gd	mb	ob
00000							3	
00001							2	
00010	18	19	3			15	7	8
00011	18	6					12	1
00100		18					2	6
00101	1	1						18
00110	2	7	11		10	1		
00111		2					7	
01000						15		
01001						16		
01010							1	
01100			1	1		4		
01101				7				
01110			1	4		5		
01111				8		1		
10000				4				
10001			2	2		1		
10010						4		
10011			2			2	4	
10100			10					
10101			11					
10110		1	10					
10111			2		1			
11000				9				
11001				4		1		
11010						2	2	
11011				1				
111--						2		
Total	39	54	53	40	11	70	40	33

b]

Twinspan group	quadrats by position				
	b	e	m	p	t
00000		1	2		
00001		1			1
00010	49		14	2	5
00011	5	4	12		16
00100	2	3	11		10
00101	5				15
00110	21	5	4		1
00111	2	3	2		2
01000	2			3	10
01001				15	1
01010			1		
01100	5		1		
01101	6		1		
01110	2		2		6
01111	4		5		
10000			1		3
10001	2		1		2
10010	1				3
10011	1	2	3		2
10100	1		7		2
10101			2		9
10110	4	1	6		
10111	1		2		
11000				9	
11001				1	4
11010	1		1		2
11011					1
111--					2
Total	115	20	78	30	97

When the sites are grouped by position (Table 3.13 b) the same two divisions that were identified in Table 3.13a, 01000 and 01001, are linked to the top and plateau quadrats of Greendykes respectively. Despite most species being recorded in both positions several grassland species (*Dactylis glomerata*, *Arrhenatherum elatius*, *Plantago lanceolata*, *Heracleum sphondylium*) had considerably higher abundance in the plateau quadrats than in the top quadrats. Also some species that are associated with disturbed ground were recorded only in the top quadrats (*Reseda luteola*, *Senecio viscosus*, *Myosotis arvensis*). This convincingly separates the vegetation on the stable plateau from the vegetation on the sloping sides near the top of Greendykes bing.

Quadrat groups 10100, 10101, 10110 and 10111 (within the 101 3rd level division) contained 33 of the 53 quadrats recorded at Clapperton (all positions are represented), plus one quadrat from Addiewell south and one from Drumshoreland south. These groups are predominantly composed of weedy species that are associated with disturbed habitats and are matched to NVC vegetation types OV10 or OV19 when entered into ComKey. The main species linking the groups are *Senecio viscosus*, *Reseda luteola*, *Cerastium glomeratum* and *Tripleurospermum inodorum*. All are annual or biennial, R or R/*[4] strategists and associated with pH levels of 6 or greater (Hodgson *et al.*, 1995) and with indicator values R=6-8 and N=5/6 (Hill, *et al.*, 1999). This species combination indicates higher nutrient availability in a basic substrate. These four species also appear together in the only robust TWINSPAN species grouping by C-S-R strategy,11101, a group that contains 12 of the 22 R and R/* strategists (Table 3.14).

Quadrat groups 01001(Greendykes) and 11000 (Drumshoreland north) held only plateau quadrats from unmanaged bings (Table 3.13 b) however the two locations varied considerably. Quadrat group 01001, Greendykes plateau, was covered in continuous vegetation and keyed out to NVC type CG2, whereas there was a high

[4] The asterisks in this section have the same function as those in a Boolean search. They represent any of the possible suffixes that can occur with the specified prefix letter within C-S-R functional groups.

percentage of bare ground at Drumshoreland north plateau (11000). This was a group of species poor quadrats containing *Sagina procumbens,* an indicator of salinity (Hill, *et al.*, 1999) that matched OV10 when keyed into ComKey.

Table 3.14 TWINSPAN groupings of individual species by C-S-R strategy

The species allocated to each C-S-R strategy type are allocated to the TWINSPAN species groups. The first 3 (of 5) levels of division in TWINSPAN are indicated 1st level ═══ 2nd level ——— 3rd level - - - -

Twin-span group	C-S-R strategies allocated to each species																					Grand Total
	c	c/ cr	c/ csr	c/ sc	cr	cr/ csr	csr	r	r/ cr	r/ csr	r/ sr	s	s/ csr	s/ csr	s/ sc	sc	sc/ csr	sr	sr/ csr	x		
00000	1				1				1													3
00100			2		1							1						1				5
01000						1	2			1												4
01010			1				3							1		1						6
01011			1	1	1											1		2		2		8
01100				1	1	2	4	1		1	1	1	1	1	1					2		17
01101	1	1	1	1	2		2							1		7			1	6		23
01110					2									1			1		1	1		6
01111								1														1
10000	1						1															2
10100	1																					1
10101	1								1		1									1		4
10110					2																	2
11000					1					1										1		3
11100					1																	1
11101								7	1	2	2											12
11110																		1				1
11111										1												1
Grand Total	5	1	5	3	12	3	12	9	3	6	4	2	1	4	1	9	1	4	2	13		100

Quadrat group 00101 accounted for 18 of the 33 quadrats for Oakbank, plus one each from Addiewell north and south. Fifteen of these quadrats were from top positions and five from the base. These groups were dominated by species present in the commercial grassland/wildflower seed mixtures that were sown on these sites during reclamation (Appendix 1): *Poa trivialis*, *Sanguisorba minor* and *Trifolium pratense.* The best NVC vegetation match was CG2.

Quadrat groups 01100, 01101, 01110 and 01111 contained 20 of the 40 Drumshoreland north quadrats plus 10 quadrats from Greendykes. The groups were recognised by *Chamerion angustifolium*, *Tussilago farfara* and *Holcus mollis*. These

are all perennials, C or C/* strategists but with a wide range of indicator values for both R and N (3-6). The groups fitted a variety of NVC types as best match (MG1, CG3, OV23 and W24) but the next best matches were all SD8 or SD7 suggesting that there was a higher degree of disturbance in these areas preventing a more stable vegetation type (or types) from developing (Tables linking TWINSPAN quadrat groupings with the NVC matches from different co-efficients can be seen in Appendix 14).

Although TWINSPAN did not use environmental factors in the analysis of the data there appeared to be some indication that the species groupings were related to features of the physics and chemistry of the substrate but particularly that there were differences between bings. The TWINSPAN quadrat groupings were quite robust in some divisions, linking very clearly to sites, positions or positions-on-site although the TWINSPAN species groupings (with two exceptions) were not obviously representative of any formal classifications (NVC or C-S-R).

3.5 Discussion and Conclusions

The lack of previous research on the West Lothian shale bings has made it difficult to approach this project with clearly defined ideas of what to expect, of both the bing sites and the vegetation growing on them. The assumption has been made that any vegetation growing on the bings has colonised by natural processes or with unintentional anthropogenic interference, and that this is primary succession, unless there are specific planting records in the West Lothian Council archives. The variety of plant assemblages recorded does not appear to be limited by the species depauperate vegetation of the surrounding agricultural and urban landscape despite the nineteen bing sites sharing a common local (West Lothian) propagule source.

Literature suggests that early colonisers will have highly dispersible propagules, early reproduction, high allocation of resources to reproduction and large numbers of offspring, and will be wind dispersed annuals. This assumption is based on MacArthur and Wilson's (2001) density dependant model (*r*- and *K*-selection) and would presume a predominance of R-strategist species (Grime, 1974). This was not

the case however. Both the pre-survey records and the baseline survey showed that although the majority of common species on the bings were wind dispersed, they were also perennials. However interpretation from literature can distort the meaning of the original. The mechanism conferring high *r* can be either high fecundity or early reproduction or a low rate of mortality. MacArthur and Wilson stated that " it is clear that the good colonizer has a large *r*, which is achieved by a low mortality rate rather than a high birth rate". Grubb (1987) elaborated on this theory and proposed that short lived, highly fecund species would only be found on stable sites with adequate water and nutrient resources. If sites were unstable or had inadequate resources then species would be long lived, and in combination sites (e.g. lava flows and shingle) pioneers would be both long and short-lived species. This would seem to explain the situation on the shale-bings where there is a combination of strongly competitive species and ruderals.

The initial investigations of this study indicated that nutrient availability might be patchy within sites. Many of the sites have unstable or frequently disturbed areas either from steep slopes or recreational use. Grubb (1987) asserts that the dipersibility of species is significant to colonisation ability, also plants that are more tolerant of lower nutrient availability are best suited to early succession. In physically unstable sites vegetative propagules are important to colonisation success. More detailed investigation of the mechanisms of dispersal in individual species in relation to the areas where they were recorded is required to test whether this assumption is true of the bing sites.

Some general hypotheses on the requirements of recorded species, as determined by indicator values (Hill *et al*, 1999), and the bing substrate have been suggested by the pre-survey investigations (Section 3.2).

- There is a strong requirement for light by most colonising plant species.
- There is a wide range of pH in the substrate, from acid to alkaline.
- There is a wide range of nitrogen availability, from poor to rich.
- The substrate is mainly free draining to the point of dryness.

The baseline survey classifications supported these postulates and identified a wide range of species groups and plant communities growing on the shale substrate of the bings, but were unable to allocate the groups to standard types or communities. The evidence from the classifications demonstrated that the bing habitat was not a single plant community, nor were individual bings discrete communities. Frequency of occurrence of species as a measurement of species composition indicated that bings were not homogeneous sites and that plant communities, if they were present, were occurring at a smaller scale than position-on-bing.

The vagaries of the different frequency lists (Tables 3.6, 3.7 and Grime, 1986) highlighted the potential dangers of drawing conclusions about the structure of vegetation based on dominant species in industrial spoil habitats. The frequency of occurrence of individual species however, both dominant and rarely recorded, raised potentially interesting questions about distribution patterns and their causes. Patterns in vegetation were shown to have a relationship to spatial distribution and frequency of individual species, information that was not available from pre-survey data. There were small groups of plant species that appeared to be indicative of distinct limiting factors within the measured environmental ranges (section 3.4.1). The results suggested that species associations were influenced by environmental features. Altitude, angle of slope and aspect of bing surfaces and percentage of bare ground recorded in quadrats may be important factors in the outcome of vegetation patterns. The collection of further environmental data, including pH and soil nutrients, may show more obvious clines in vegetation relating to these gradients.

3.5.1 Summary

The initial objectives of this study were to detect any recognisable patterns in the vegetation and to ascertain whether the resulting species associations represented plant communities recognised elsewhere in Britain, as outlined in the introductory paragraph of this chapter. Species associations did not appear to equate with standard vegetation types or classification. However, recurring species groupings and irregularities in individual species abundance and distribution were identified and these varied both between and within different bing sites providing an

identifiable structure to the vegetation. The assigned ecological traits of the species associations within the vegetation indicated that this could be due to considerable variation in the physical and chemical habitat. This generated the hypothesis that species associations and variations in individual species abundance will follow measurable gradients in the physical or chemical environment.

CHAPTER FOUR

"All seeds which land on the soil do not find conditions suitable for establishment."

J.L. Harper *et al.* (1961) The Evolution and ecology of closely linked species living in the same area. *Evolution*, 15, p217.

4 The Association of Plant Species and Communities with the Physical and Chemical Environment

The classification and ordination of species data in Chapter Three demonstrated that there are distinct groups and associations of species in the vegetation of the West Lothian shale bings but that these do not conform to phytosociological patterns described in literature (Rodwell, 1991a; 1991b; 1992; 1995; 2000)). There were strong indications from the shared habits (as described by Hill *et al.*, 1999; Hodgson *et al.*, 1995) of individual species recorded together that the burnt shale substrate of the bings is neither homogeneous within nor between sites, although the spoil originated from a single shale bed and was treated using the same industrial processes. This chapter relates the vegetation survey data described in the previous chapter to measured physical environmental factors of angle of slope, bare ground, elevation (derived from position on site as described in Chapter Three, Section 3.3.1), aspect and management, and the chemical environmental factors of pH, nitrogen, phosphorus, potassium, magnesium, sodium and calcium. The study set out to define the extent of the physical and chemical variation within and between sites and to determine what influence, if any, the variation had on vegetation patterns, and the distribution of individual species and species associations recorded in the field. The aims were to answer the questions proposed in Chapter One:

Are vegetation patterns associated with environmental gradients?

How limiting is the absence of soil, in the biological sense, to the colonisation process on shale bings?

Does species composition reflect gradients in either the chemical or physical environment?

The physical features of elevation, aspect and management were used to describe the topography and stage of succession of individual bings (where possible) and to identify the position of individual recording quadrats within the sites. Vegetation data were then linked to large-scale site topography. Angle of slope and percentage bare ground were used to identify individual species and associations that were recorded within limited physical ranges. Small-scale variation within the larger physical divisions could then be identified.

The extent of variation in the chemical environment was measured at the quadrat level within defined positions on the bings. Aspects of topography and species distribution were then linked to the variations in individual nutrients and pH.

4.1 The Shale Substrate

As described in Chapter Two, Section 2.5 many of the physical properties of burnt oil-shale spoil are similar to those of other types of large scale industrial waste (Table 4.1). The shale bings are made of a single material, with a surface structure unlike normal soils. In common with all primary succession sites they initially have no organic matter and no microbial activity (Bradshaw & Chadwick, 1980). The bings, like other spoil heaps, suffer from surface instability caused by a combination of topography and lack of vegetation. This is exacerbated by a substrate consisting of coarse particles which are easily blown by the wind when dry and eroded by heavy rain when wet (Bradshaw & Chadwick, 1980). The major effects of water erosion are the break down of the laminar structure of shale and the movement of small particles from the surface of the substrate but the steep slopes and height of many of the bings (Appendix 1) can occasionally intensify the effect, leading to the formation of gullies and minor landslips.

In many regions of the World the establishment and development of vegetation on spoil heaps is severely affected by drought, due to the large particle size of the substrate and its low water holding capacity. Long-term average rainfall, exceeding

40 mm every month throughout the year[1] (Meteorological Office, 2004a), ensures that this is not a great problem in central Scotland. Lack of existing vegetation can, however, result in rapid, short-term, surface desiccation from both sun and wind, consequently making conditions difficult for early colonisers and continuing seedling establishment (Bradshaw & Chadwick, 1980). The combined factors of altitude and lack of vegetation, as are found on the bings, can also result in unpredictable wind and weather patterns at ground level causing soil structure to vary over small distances (Urbanska *et al.*, 1998).

There are no published data on the physical and chemical properties of the substrate that forms the West Lothian oil-shale bings. Bradshaw and Chadwick (1980) compared the physical and chemical characteristics of different types of derelict land material (Table 4.1) and suggested that the physical substrate of oil-shale bings is not expected to vary greatly from other types of spoil apart from urban waste. Although their information on oil-shale waste was based on north American strip mined sites the same retorting process is used to extract the oil and should result in waste that is comparable with that found in the bings in Scotland.

The chemical properties of oil-shale waste differ from other types of waste to a greater extent than the physical properties (Bradshaw and Chadwick, 1980). It is expected that there will be a severe deficiency of macronutrients, adequate micronutrients and a moderate excess of salinity in the substrate. The bings ought to have a moderate deficiency[2] in pH, making them slightly acidic, but should not contain heavy metals or other toxins (Table 4.1). However, in a later section of their text Bradshaw and Chadwick (1980) suggest that spent shale will initially have a high pH due to high concentrations of soluble salts. The rainfall in central Scotland

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[1] The rainfall data is from the nearest meteorological recording station at Edinburgh airport: Greendykes is only 6.5 kilometres to the west but Addiewell is 20 kilometres to the west. Rainfall increases from east to west in central Scotland therefore the actual rainfall in West Lothian will be higher. Long-term average rainfall for Stirling, 40 kilometres to the north-west of Edinburgh airport, exceeds 50 mm every month throughout the year.

[2] Bradshaw and Chadwick record a severe deficiency of pH in both colliery spoil and strip mining and describe these as acidic, therefore moderate deficiency is presumed to be slightly acidic.

is sufficient to leach out most of the soluble nutrients (e.g. potassium and sodium) therefore it is unlikely that they will occur at high levels after 30 years, the minimum time since cessation of dumping.

Table 4.1 The physical and chemical characteristics of derelict land material

The physical and chemical characteristics of derelict land material (adapted from Bradshaw and Chadwick, 1980).
Deficiency: severe OOO moderate OO slight O adequate o
Excess: severe +++ moderate ++ slight +
(Relative to the establishment of a soil/ plant ecosystem appropriate to the material: variations in severity are due to variation in materials and situations.)

materials	texture & structure	stability	water supply	surface temp-erature	macro nut-rients	micro nut-rients	pH	toxic mater-ials	salinity
oil shale	OO	OOO/o	OO	o/++	OOO	o	OO/o	o	o/++
colliery spoil	OOO	OOO/o	O/o	o/+++	OOO	o	OOO/o	o	o/++
china clay	OOO	OO	OO	o	OOO	o	O	o	o
strip mining	OOO/o	OOO/o	OO/o	o/+++	OOO/o	o	OOO/o	o	o/++
urban waste	OOO/o	o	o	o	OO	o	o	o/++	o
coastal sands	OO/o	OOO/o	O/o	o	OOO	o	o	o	o/+
road-sides	OOO/o	OOO	OO/o	O/o	OO	o	O/o	o	o/++

Nitrogen is considered to be the most important of the macronutrients. Cowles recognised nitrogen as one of the principal limiting resources in terrestrial primary succession on sand dunes in 1899. The constraint of low nitrogen availability results in early dominants that are generally capable of nitrogen fixation (Sprent, 1993), however this is dependent on pH. Nitrogen fixation by free-living organisms (*Azotobacter* and *Clostridium*) and symbiotic organisms (*Rhizobium* and *Actinomyces*) are favoured at high levels of pH when bacteria are more abundant (Mengel and Kirkby, 1982). pH (potential of hydrogen) affects the availability of many nutrients, and plants vary widely in their sensitivity to soil pH.

Bradshaw and Chadwick (1980) present a range of macronutrient levels required for "normal plant growth" when restoring land. The levels are geared towards growth of agricultural crops and pasture and not wholly relevant to naturally occurring ecosystems. They do not, however, represent recommended fertiliser applications

for maximum productivity like most published information on plant nutrition and therefore provide a standard that can be used for comparison with any new data collected (the levels are presented in Section 4.4 Table 4.14 on page 106).

Sodium is not considered to be an essential plant nutrient. High levels can destroy soil structure, reduce plant growth and are associated with high pH. Bradshaw and Chadwick (1980) do not give an optimum range for sodium concentration but commercial sources agree that more than 120 ppm is detrimental to the growth of many plant species (Agvise, undated; Green Air Products, undated). Availability of magnesium, potassium and phosphorus all reduce with high pH (Mengel and Kirkby, 1982). Very low levels of these nutrients are likely to cause low production in plants. Calcium levels are generally higher in association with pH >6 but need to reach 20,000 ppm to become detrimental to plants (Agvise, undated), this is a factor of ten greater than the maximum level suggested for normal plant growth by Bradshaw and Chadwick (1980).

The literature is open to various interpretations making expected availability of the various nutrients on oil shale bings very difficult to predict. This in turn leads to difficulties in predicting how vegetation might be influenced by variations in the chemical environment. Rees and Bergelson (1997) recognised that low nutrient, low disturbance habitats tend to have successions running from light specialists to nutrient specialists and that high nutrient, high disturbance habitats have opposite successions. Existing information on the shale bing sites indicated a predominance of low nutrient, high disturbance habitats making any predetermination of the composition of vegetation communities problematic. It has been suggested that plants from infertile soils will have inherently slow growth rates (Parsons, 1968). These slow growing species will be at a selective advantage on infertile soils because they will not out-grow the available nutrient supplies.

4.2 Collecting, Preparing and Analysing the Data

Physical environmental data were collected in conjunction with floristic information from eight bing sites in the baseline survey (Chapter Three, Section 3.3.1).

Percentage bare ground, aspect, angle of slope and elevation (measured as position) were recorded for each of the 340 quadrats. Some of the most frequent species appeared to be limited by physical environmental criteria and were only recorded within particular ranges of bare ground, aspect, angle of slope and position over all of the bing sites. Other, less frequent, species were recorded on all sites and all positions within sites (Chapter Three, Section 3.4). To determine the extent to which vegetation composition might be interrelated with clines in the physical environment the species recorded in the baseline survey were first classified by each environmental gradient independently. By utilising autecological information for individual species recorded as representative of divisions within any of the measured physical factors an indication of particular species habits associated with that factor can be calculated. The association between the physical environment and plant traits (annual and perennial life history, established strategy and mode of dispersal) were tested with χ^2. The quadrat data are treated as statistically independent with respect to bing sites throughout the chapter. Although there will be some degree of pseudoreplication in the data due to non-demonic intrusions (Hurlbert, 1984), unmeasurable and/or unknown chance events that may affect species composition or environmental gradients, the impact on the validity of the analyses was felt to be insignificant.

The chemical environmental data were collected from a series of 50 fixed quadrats on only four of the bing sites used in the baseline survey due to time constraints. The four bings were selected to represent the range of size and management strategies recorded in Appendix 1. Clapperton, a newly managed site, Oakbank, a well established managed site, Greendykes, a large unmanaged site, and Mid Breich, a small unmanaged site. The fixed quadrats were contiguous blocks of four 2 m × 2 m quadrats from the same vegetation type and were established as extensions of quadrats from the baseline survey. There were four random blocks at the top (only 2 at Mid Breich because of its small size), middle and base of each bing, plus four from Greendykes plateau, representing the range of elevations and aspects found at the four sites (50 in total). Floristic and physical environmental data were recorded at the same time as substrate samples were collected from the four quadrat blocks on

Greendykes middle slopes, as this position had not been part of the baseline survey (Chapter Three, Section 3.3.1).

The substrate samples for soil analyses were collected in early spring (Thomson *et al.*, 1997). Ten spots were selected at random from within the quadrat block (Gemmel, 1977). The surface vegetation was removed and each sample was split into two. Trowel-sized samples were collected from the top 50 mm of substrate and the lower, unweathered substrate. The 10 top samples and 10 bottom samples from each quadrat were then bulked resulting in two bulked samples for each of the quadrat positions at all four bings (100 in total). Each fresh bulked sample was passed through a 2 mm sieve to remove large stones, root fragments and to provide homogenous samples. 50 g of the sifted material from each sample was retained for chemical analysis. The remainder was reduced by washing through a 0.2 mm sieve (ter Heerdt *et al.*, 1996) to remove clay and silt and provide concentrated 250 g samples for a controlled glasshouse trial to be described in Chapter Five.

4.2.1 Physical analyses

The baseline survey of 340 quadrat samples contained 211 species (see Chapter Three) and resulted in a matrix of 4,267 entries. The full data set was used for grouping and classification of the species in relation to the physical environmental data. Each of the physical features was investigated individually in the first instance.

The measure of elevation was taken from the position of the recording quadrats on the bing sites, plateau, top, middle, base and excavation as described in Chapter Three. The data were allocated to three divisions; Upper = plateau and top quadrats combined, Middle = middle quadrats, Lower = base and excavation quadrats combined.

Aspect was measured in degrees from magnetic North (as described in Chapter Three) but quadrats were allocated to two divisions, those recorded from $315<135^{o}$ (NW to SE) and those recorded from $135<315^{o}$ (SE to NW). Data of species by aspect were collected as degrees from north (to the nearest 5^{o}) and the divisions could reasonably have been presented as a series of polar graphs. Preliminary

analyses suggested that when investigating the over all distribution patterns of vegetation this level of detail was not necessary for comparison with the broadly measured divisions of the other physical environmental features, although it could prove to be applicable when researching individual species. The most extensive comparable work from literature (Grime *et al*, 1988) divided species between north and south aspects and whether they were shaded or not. On the bing sites this did not seem to be the most logical split because of the direction of the prevailing winds (Figure 4.1) and lack of cover. The wind is directed by the south-west to north-east alignment of the Pentland Hills and is channelled through the River Almond valley (on the same alignment). The main wind frequencies (> 55% in November; ≈ 40% in May) are therefore between 210 and 270°, compounding the desiccating effect of higher solar radiation on the south and west facing slopes (Meteorological Office, Edinburgh, 1990).

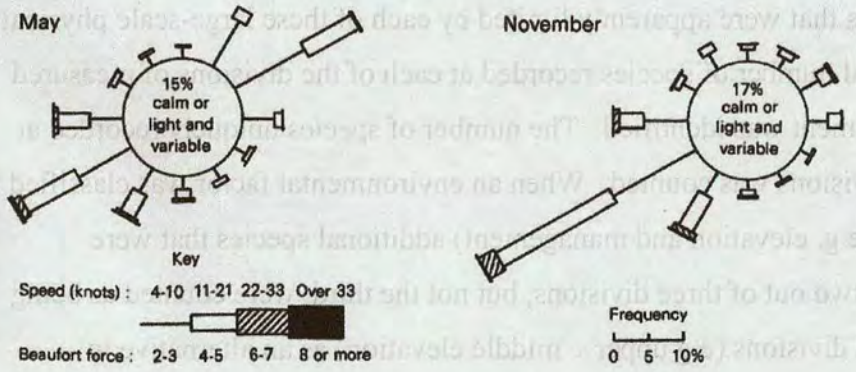

Figure 4.1 Wind-roses for Edinburgh Airport

The wind-roses indicate the wind directions in May and November, predominantly from 210-270°. Increased length of arm denotes increased frequency of winds and increased shading of arm denotes greater strength of winds (adapted from Meteorological Office, Edinburgh, [1990] using data for Edinburgh Airport).

Management practices carried out from cessation of dumping at each site[3] were used as a further large-scale division of the data. Quadrats were grouped according to the degree of management and length of time elapsed since management in the recording

[3] This varies between sites from 1915 – 1962 (Appendix 1)

area using the information available from Council records (West Lothian, various) and summarised in Appendix 1. This allowed quadrats within a bing to be allocated to one of three different management divisions. Unmanaged sites, where there was no record of any reshaping, seeding or planting, were represented by quadrats recorded on Greendykes, Mid Breich (except for quadrats recorded in the excavated area which had been managed) and Drumshoreland south base. Quadrats recorded on Addiewell south (except for the excavated area), Addiewell north and Oakbank represent 'old' managed sites that were reshaped, ameliorated, seeded and planted more than 10 years ago (before 1993). The remaining quadrats recorded on Clapperton, Drumshoreland north and the excavated areas at Addiewell south and Mid Breich are 'new' managed sites that have been reshaped and/or planted within the last five years (since 1998).

The recorded distribution of species over all 8 sites was used to identify species and groups of species that were apparently limited by each of these large-scale physical factors. The total number of species recorded at each of the divisions of measured physical environment was identified. The number of species uniquely recorded at each of these divisions was counted. When an environmental factor was classified in three divisions (e.g. elevation and management) additional species that were recorded in any two out of three divisions, but not the third, were counted as being unique to shared divisions (e.g upper + middle elevation) as an alternative to introducing divisions of disassociation.

Strongly associated species were calculated to include information on species that were not unique to a division but were recorded there more frequently than in other divisions. A species was considered to have a strong association with one of the divisions if the frequency of records in that division was equal to or more than two times the frequency of records in the other division, or in each of the other two divisions for elevation and management (i.e. ≥2:1:1). Using a χ^2 test the difference between random distributions over the three divisions and this ratio is statistically significant in species that are recorded in 15 or more quadrats although statisticians do not consider the test to be valid on matrices where more than 20% of cells have expected values of less than 5 (Ramsey and Schafer, 1997). Thus a species could

also have a strong association if the number of records in each of two divisions was double, or more, the records in the third elevation (e.g. *Centaurea nigra* was recorded in 34 upper, 8 middle and 39 lower quadrats and was counted as having strong association with the upper + lower division to represent a strong dissociation from the middle division). The strong association of some species to particular division(s) of the physical environment was considered to be an important additional indicator of the extent that these factors influence the patterns of vegetation, particularly when the distribution of abundant and frequently recorded species like *Centaurea nigra* were apparently limited.

Monte Carlo analysis of randomisation, a program written by Legg (unpublished), was used to test if the number of unique species in a subset of the quadrats was significantly different from the number of unique species that would be expected if there were no association between the distribution of species and the basis for the selection of the subset. The analysis takes the actual full set of quadrat data being tested and extracts a similar-sized subset of quadrats at random (without replacement). The number of unique species in this random subset is calculated. This process is repeated many (10,000) times and the frequency distribution of the numbers of unique species is accumulated. The observed number of unique species is then compared with this modelled distribution. If the observed value is within the range that contains the 95 percentile of the modelled values then this is deemed to be consistent with the null model of no association, while observed values outside this range are considered significantly different from expected ($P < 0.05$). A similar analysis for strongly associated species tested the observed number against the modelled distribution of strongly associated species obtained from the repeated random selection of quadrats as above. For this analysis it was sometimes necessary to construct three subsets of quadrats from the full data set so that the definition of 'strongly associated' species in the modelled data was the same as that described in the previous paragraph. This analysis was used to show, with statistical significance, whether or not groups of species that seemed to be restricted to any particular environmental criterion could have occurred by chance.

The species allocated to each group were then categorised by their expected affiliation to pH (high or low), lifestyle (annual or perennial), established strategy (ruderal or stress tolerant) and mode of dispersal (unspecified, wind or animal) (Hodgson *et al.*, 1995). χ^2, supported by G-test for contingency tables with any number of rows or columns, and Fisher's Exact test for 2 x 2 tables (Legg, 2004), was calculated using the number of species associated with each of these autecological habits to demonstrate if any variation between groups of species linked to each of the divisions of elevation was statistically significant. Species that were not associated with any of the divisions were included in the χ^2 matrix as an additional division.

The measured angles of slope (0-80°) and percentage bare ground (0-100%) recorded in each quadrat and their associated vegetation were analysed by the same method to show if species were limited by these factors within the larger topographical and management divisions.

It was not always statistically sound to use the full data set (henceforth referred to as the baseline data set) for analyses as many of the species appeared in fewer quadrats than there were divisions in the sets of physical environmental data. A secondary data set was therefore constructed using only species recorded in nine or more quadrats (species recorded in ≤8 quadrats were removed from the data set). This left a total of 104 more frequent species (henceforth referred to as the most frequent data set) that could (mathematically) each be present at all elevations (5 positions), all aspects (the four points of the compass and the four quarters) and on every site (8 sites). A full list of the frequently recorded species is presented with autecological information in Table 4.13 (after Section 4.2.3 page 100).

4.2.2 Chemical analyses

The samples of fresh sieved substrate (section 4.2) were analysed for calcium, sodium, phosphorus, potassium, magnesium and nitrogen by Mr A. N. Gray[4].

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[4] Senior Analytical Technician, Institute of Atmospheric and Environmental Science, School of GeoSciences, the University of Edinburgh.

Nitrogen was extracted from the substrate with 1 M KCl. 10 grams of each sample was weighed into plastic bottles and 200 ml of 1 M KCl added. Bottles were capped and shaken on a mechanical shaker for 2 hours. 15 ml of the extract was measured into graduated centrifuge tubes and centrifuged at 5000 rpm for 20 minutes. The resulting supernatant liquid was retained for analysis for nitrate (NO_3^--N) and ammonium (NH_4^+-N). Calcium, sodium, phosphorus, potassium and magnesium were extracted by the same method using 2.5% acetic acid as the extractant. Automated colorimetric analysis was used to measure extractable phosphorus, NO_3^--N and NH_4^+-N using a Bran + Luebbe Auto Analyzer 3, continuous flow analyser (Application Notes G-109-94 row 3 [NO_3^--N] G-103-93 row 1 [P] G-102-93 row1 [NH_4^+-N]). Extractable calcium, sodium, potassium and magnesium were determined by flame atomic absorption spectroscopy (FAAS) using a Unicam MS series spectrometer.

Soil pH was measured by glass electrode in a solution of 1 volume of soil to 2 volumes of distilled water with a Russell (Auchtermuchty) pH meter.

Bradshaw and Chadwick's (1980) ranges of nutrient requirements for normal plant growth were considered most suitable for comparisons with field conditions, as described in Section 4.1. These are presented in parts per million (ppm) in the extracted solution therefore the results of the bing substrate analyses (with the exception of pH) were converted to ppm for direct comparison. Alternative nutrient requirements available from literature were based on horticultural and agricultural requirements for crop nutrition, yield response and related to optimum fertiliser applications (Agvise Laboratories, undated; Green Air Products, undated; Mengel and Kirkby, 1982).

4.2.3 Multivariate statistical analyses

Multivariate analysis techniques were used to demonstrate any combined effects of both the measured physical environmental variables and the measured chemical environmental variables and the extent to which each of them were associated with the variation in vegetation patterns. The data set containing the most frequent

species and the complete baseline data set were analysed separately to determine any advantages or disadvantages in retaining rare species in analyses.

There are several methods of treating multivariate data. All correspondence analyses make the assumption that there is an environmental gradient and that this will be reflected in the first axis. Principal Component Analysis (PCA) was inappropriate because the responses from individual species to the environmental gradients were not linear (gradient length was more than four standard deviations indicating a unimodal response) (ter Braak and Šmilauer, 2002). Distance along the axis reflects the degree of dissimilarity in species composition. However the increased differentiation can cause arch effect, because after a certain distance along the axis all points will have no species in common with the original point, and the second axis only measures the strength of the arch. For this reason the initial test used was Detrended Correspondence Analysis (DCA) (Hill and Gauch, 1980). Detrending the data straightens the arch and rescales the points in the same order as the environmental gradient making DCA the most appropriate analysis for the data. DCA is geared towards ecological data based on samples and species presented in a matrix and although often used to generate hypotheses it can also be used to support or reject hypotheses based on observation (McCune and Mefford, 1997). The analysis has the advantage that a second matrix containing measured environmental data can be superimposed over a graphical representation of the ordination to help identify the main (unnamed) axes of the DCA. It was not considered necessary to transform the percentage cover data when carrying out this analysis. Canonical Correspondence Analysis (CCA) was then used to constrain the initial ordination by multiple regression on the measured environmental variables contained in a second matrix. CCA weights samples according to the number of species they contain and this means that the distinctiveness of samples with several rare species becomes exaggerated. Many researchers exclude rare species from the analysis for this reason (Zuur *et al.*, 2003) or transform the data to boost the influence of rare species in the ordination (Sieber *et al.*, 1998). The sensitivity of CCA to outliers can effectively be used to verify data and identify groups of variables that will discriminate between samples. Again it was decided not to manipulate the data.

The DCA and CCA analyses were performed using CANOCO 4.5 (ter Braak and Šmilauer, 2002). The analyses were set up as projects in CANOCO using the default selections throughout. DCA of species data only was detretended by segments with no transformation of species percentage cover data, no weighting of species or samples and no downweighting of rare species, then repeated with the addition of supplementary environmental data. CCA of species and environmental data was based on the DCA analysis. The selected options were to extract patterns from the explained variation only, using biplot scaling with no transformation of species data, no environmental variables deleted and no forward selection. CANOCO was also set up to perform Monte Carlo permutation tests based on the first ordination axis and then on all of the canonical axes using the full model over 499 permutations.

4.3 Plant Species Distributions

Plant species distributions with respect to each of the recorded physical parameters were initially calculated using both the baseline data set and the most frequent data set, as described in Section 4.2.1. The most frequent species are listed individually at the end of this section with the recorded limits of measured physical environment and autoecological information for each species (Table 4.13, page 100). The results of ordination by chemical parameters and multivariate analyses of all data are recorded in separate sections (4.4 and 4.5).

4.3.1 Elevation

The total number of species recorded at each of the upper, middle and lower divisions of elevations were identified using the baseline data (211 species). Species were allocated to one of the divisions or shared divisions if they were uniquely recorded or statistically strongly associated with that division as described in Section 4.2.1. If a species was recorded at all elevations and not strongly associated with any category of division it was considered to have no association. No species were allocated to more than one category of division. Thus species could be allocated to any of 13 possible categories of elevation.

1. Species recorded only at the upper elevation

2. Additional species with strong association to upper elevation
3. Species recorded only at the middle elevation
4. Additional species with strong association to middle elevation
5. Species recorded only at the lower elevation
6. Additional species with strong association to lower elevation
7. Species recorded only at upper and middle elevations
8. Additional species with strong association to upper and middle elevations
9. Species only recorded at lower and middle elevations
10. Additional species with strong association to lower and middle elevations
11. Species only recorded at upper and lower elevations
12. Additional species with strong association to upper and lower elevations
13. Species with no association to any division of elevation

Sixty-one species from the baseline data were unique to a main division of elevation and a further 48 were unique to a combined division (Table 4.2a). An additional 65 species were strongly associated with either a main or combined division. Thirty-seven species had no association with any elevation.

The numbers of species associated with each of the divisions of elevation were often small and these apparently limited groups of species could be the result of chance events. Monte Carlo analysis (as described in Section 4.2.1 p82) was used to determine if the number of species unique to, or strongly associated with, each of the divisions of elevation were significantly greater or less than the number expected from the null model of no association between vegetation and elevation. From this analysis it was determined that significantly greater numbers of unique species were recorded in quadrats positioned in the lower division of elevation (indicated * in Table 4.2a) and significantly less than expected numbers of unique species in the combined upper + middle and upper + lower divisions (indicated † in Table 4.2a). All six of the groups of species deemed to be strongly associated with a division are also significantly smaller than expected.

Table 4.2 Numbers of species and quadrats by elevation

The total number of quadrats and species, including cryptogams, recorded at each of the divisions of elevation (upper, middle and lower) using a] the baseline data and b] the most frequent species data, are displayed. The numbers of species unique to, and strongly associated with, each division and combined division are also shown. The number of recorded quadrats is the same in both data sets. Monte Carlo analysis (Section 4.2.1) tested the significance of the number of species limited to a division or combined division by comparison with the number expected from the null model of no association between vegetation and elevation.
** highlights where the number of species unique to, or strongly associated with, a division of elevation is significantly ($p<0.05$) greater than the number expected.*
† highlights where the combined number of species unique to, or strongly associated with, a division of elevation is significantly ($p<0.05$) less than the number expected.

	ELEVATIONS					
	upper	middle	lower	upper + middle	lower + middle	upper + lower
a] BASELINE DATA SET (211 species in 340 quadrats)						
number of quadrats	127	78	135	205	213	262
number of species recorded	133	148	182	170	199	203
unique species	12	8	*41	†9	29	†10
strongly associated species	†14	†2	†15	†7	†8	†19
b] MOST FREQUENT DATA SET (104 species in 340 quadrats)						
number of species recorded	94	101	101	104	103	104
unique species	*1	0	0	*2	*10	2
strongly associated species	*14	2	*15	†7	†8	†19

The most frequent data (104 species recorded in 9 or more quadrats, Table 4.13) were classified and analysed by the same method (Table 4.2b) revealing significantly greater numbers of species unique to the upper (a single species, *Agrostis gigantea*, recorded in 13 of the 127 upper elevation quadrats), upper + middle and lower + middle divisions. Significantly greater numbers of species were also strongly associated with the upper and lower divisions (these are the same species that formed non-significant groups in the baseline data analysis). The groups of species strongly associated with the three combined divisions remained significantly lower than expected.

The groups of species associated with each elevation were allocated to their expected autecological habits (Hodgson *et al.*, 1995) to ascertain if there was any relationship between pH, life history, established strategy and mode of dispersal and the divisions of elevation. The habits of the 211 species recorded in the baseline data were used for comparison (all species, Table 4.3) and these suggested that there were more than

twice as many species associated with high pH than low pH and more than three times as many perennials as annuals. There were, however, similar percentages of ruderal and stress tolerant species (24% and 29%) and of the three main modes of dispersal (unspecified 30%, wind 46%, animal 24%). The species recorded in the most frequent data set (most frequent species, Table 4.3) are distributed in statistically similar proportions between the autecological habits ($p = 0.914$).

Table 4.3 Species habits associated with elevation

Species solely and strongly associated with each of the elevation divisions and those species with no apparent association to any elevation, that share particular autecological habits, are presented as percentages. This demonstrates the variability of species type associated with different elevations (upper, upper + middle, middle, lower + middle, lower, upper + lower, from Table 4.2a). The percentages of all species and the most frequent species, recorded on the bings that share the same habit are also presented. Autecological values were adapted from Hodgson et al. *(1995).*

Experiment-wise χ^2 (contingency tables with seven rows and two or three columns) has been calculated between the divisions of elevation by comparing the numbers of species (presented as percentage in the table) in the columns representing each of the ranges of autecological habit, pH, life history, established strategy and mode of dispersal. $P<0.05$ demonstrates a significant deviance from the expected in the distribution of species between the columns

A comparison-wise χ^2 (2x2 or 2x3 table) has been calculated within each autecological habit to test for significant deviance in the proportion of species recorded at individual elevations from the numbers recorded for all species(indicated by †).

Habit / elevation	no. of spp	pH		Life history		Established strategy		Mode of dispersal		
		>6	<5	annual	perennial	R*	S*	unsp.	wind	animal
upper	26	27	8	†46	†54	35	23	38	46	16
upper/mid	16	19	19	38	62	44	25	50	44	6
middle	10	30	10	10	90	10	20	10	70	20
lower/mid	37	30	19	11	89	†5	†30	30	38	32
lower	56	34	9	11	89	14	14	46	33	21
upper/low	29	†55	†3	14	86	17	31	31	41	28
no assoc'n	37	†5	†19	16	84	21	21	†0	†68	†32
all species	211	37	16	22	78	24	29	30	46	24
mostfreq't	104	35	13	27	73	27	24	36	37	27
χ^2		17.617		21.769		8.468		33.244		
p		0.007		0.001		0.206		0.001		

The columns representing each of the ranges of autecological habit were compared using an experiment-wise χ^2 calculation (described in Section 4.2.1.) to determine any significant deviation from the expected distribution of species between the columns as explained in the legend of Table 4.3. The analysis revealed significant variation in pH, life history and mode of dispersal associated with divisions of elevation.

A similar comparison-wise χ^2 was then calculated within each habit to test for significant deviation in the proportion of species recorded at individual divisions of elevation from the numbers recorded for all species (Section 4.2.1 and Table 4.3). The analysis recognized significant deviations in individual divisions of elevation associated with pH (upper + lower and no association), life history (upper) and mode of dispersal (no association) that explain the identified experiment-wise variation. χ^2 also identified a significant deviance in the proportion of species recorded at the lower + middle elevations from the numbers recorded for all species for R* and S*, established strategy, although there was no significant deviation between the two columns.

4.3.2 Aspect

As described in Section 4.2.1 the 211 species recorded on the bings were divided by their occurrence in quadrats sampled in either the north and east facing aspects (192 quadrats) or the south and west facing aspects (148 quadrats). The species in the base data were allocated to one of the divisions if they were uniquely recorded or statistically strongly associated with that division as described in Section 4.2.1. If a species was recorded at both aspects and not strongly associated with any category of division it was considered to have no association (Table 4.4a). The numbers of species associated with the divisions of aspect were either not significant or significantly lower than expected.

The distribution of species and analysis was repeated with the frequent species data identifying two species (significantly greater than expected), *Peltigera canina* (12 quadrats) and *Calluna vulgaris* (11 quadrats), that were unique to the north and east facing aspects (Table 4.4b). The significantly lower than expected numbers of

species associated with divisions of environment seem to be compounded by the low abundance of some species (see also Tables 4.2a and 4.2b).

Table 4.4 Numbers of species and quadrats by aspect

The total number of quadrats and species, including cryptogams, recorded at each of the divisions of aspect (north and east facing or south and west facing) using a] the baseline data and b] the most frequent species data, are displayed. The numbers of species unique to and strongly associated with, each division are also shown. The number of recorded quadrats is the same in both data sets. Monte Carlo analysis (Section 4.2.1) tested the significance of the number of species limited to a division by comparison with the number expected from the null model of no association between vegetation and elevation.
** highlights where the number of species unique to, or strongly associated with, a division of aspect is significantly ($p<0.05$) greater than the number expected.*
†highlights where the number of species unique to, or strongly associated with, a division of aspect is significantly ($p<0.05$) less than the number expected.

	ASPECTS	
	north and east facing	south and west facing
a] BASELINE DATA SET (211 species in 340 quadrats)		
number of quadrats	192	148
number of species recorded	190	177
unique species	34	21
strongly associated species	†40	†13
b] MOST FREQUENT DATA SET (104 species in 340 quadrats)		
number of species recorded	104	102
unique species	*2	0
strongly associated species	22	2

The groups of species associated with each aspect were allocated to their expected autecological habits (Hodgson *et al.*, 1995) and statistically analysed, as described in Section 4.3.1 for elevation (Table 4.5). The variation between the R* and S* columns of established strategy is significant due to deviation from the expected ratio in the group of species with no association to either of the two aspects. There is also significant variance between the modes of dispersal but this cannot be linked (significantly) to any division of aspect.

Table 4.5 Species habits associated with aspect

Species solely and strongly associated with each of the aspect divisions and those species with no apparent association to either aspect, that share particular autecological habits, are presented as percentages. This demonstrates the variability of species type associated with different aspects (Table 4.4a). The percentages of all species recorded on the bings that share the same habit are also presented. The comparative data for most frequent species is not displayed in this or subsequent tables as there is no significant variance from the baseline data (all species). Autecological values were adapted from Hodgson et al. *(1995).*

Experiment-wise and comparison-wise χ^2 has been calculated between the divisions of aspect as described for divisions of elevation in the legend of Table 4.3. $P<0.05$ demonstrates a significant deviance from the expected in the distribution of species between the columns. Significant deviance in the proportion of species recorded at individual aspects from the numbers recorded for all species is indicated by †.

Habit / aspect	no. of spp	pH		Life history		Established strategy		Mode of dispersal		
		>6	<5	annual	perennial	R*	S*	unsp.	wind	animal
north and east facing	74	26	12	12	88	13	26	23	61	16
south and west facing	34	24	12	15	85	12	18	36	32	32
no assoc'n	103	33	13	24	76	†37	†22	35	38	27
all species	211	37	16	22	78	24	29	30	46	24
χ^2		0.247		4.573		6.732		12.018		
p		0.884		0.102		0.035		0.017		

4.3.3 Management

The quadrats were grouped according to the management regime of the area of the recording site (unmanaged - with no record of any reshaping, seeding or planting; old managed - that were reshaped, ameliorated, seeded and planted before 1993; new managed - that have been reshaped and/or planted since 1998. quadrat allocation to each of the regimes is described in Section 4.2.1), resulting in six possible divisions or combined divisions: unmanaged, old managed, new managed, unmanaged + old managed, old + new managed and unmanaged + new managed. Recorded species that were unique to or strongly associated with a division or combined division were identified, as were those species with no apparent link to any division (as for elevation).

Table 4.6 Numbers of species and quadrats by management

*The total number of quadrats and species, including cryptogams, recorded at each of the divisions of management (unmanaged, old managed and new managed) using a] the baseline data and b] the most frequent species data, are displayed. The numbers of species unique to, and strongly associated with, each division and combined division are also shown. The number of recorded quadrats is the same in both data sets. Monte Carlo analysis (Section 4.2.1) tested the significance of the number of species limited to a division or combined division by comparison with the number expected from the null model of no association between vegetation and elevation. * highlights where the number of species unique to, or strongly associated with, a division of management is significantly ($p<0.05$) greater than the number expected. † highlights where the number of species unique to, or strongly associated with, a division of managemant is significantly ($p<0.05$) less than the number expected.*

	MANAGEMENT REGIMES					
	un-managed	old managed	new managed	un- + old managed	old + new managed	un- + new managed
a] BASELINE DATA SET (211 species in 340 quadrats)						
number of quadrats	111	116	113	227	229	224
number of species recorded	132	150	128	193	194	161
unique species	17	*50	18	†16	†12	†25
strongly associated species	†11	†16	†9	†5	†5	†6
b] MOST FREQUENT DATA SET (104 species in 340 quadrats)						
number of species recorded	89	83	92	100	104	97
unique species	0	*7	*4	*5	*4	*17
strongly associated species	*8	*15	*9	†6	†4	†6

The number of quadrats and number of species from the baseline data recorded from the quadrats in each of the three main management regimes were similar (Table 4.6a), however a highly significant one third (50) of species recorded on old managed sites were unique to this regime. The numbers of species unique to and strongly associated with un-managed and new managed regimes were not significant or significantly less than expected.

The numbers of unique species from the most frequent data recorded in both the old and new managed regimes and the three combined management divisions were significantly greater than expected (Table 4.6b). Despite none of the species being unique to unmanaged sites there were significantly higher than expected numbers of strongly associated species at all three divisions (unmanaged, old managed and new managed). The numbers of species strongly associated to the combined divisions, however, were significantly lower than expected.

The species associated with each of the management regimes were linked to their expected autecological habits (Hodgson *et al.*, 1995) so that any shared traits within a division could be identified (Table 4.7). The habits that showed significant variance with management were pH, life history and established strategy.

There is significant variance from pH ratio of all species in the ratio of species associated with old managed division, and a similar variance from established strategy associated with old managed (high proportion of stress tolerant species) and new managed divisions (high proportion of ruderal species). The new managed division had a single stress tolerant species, *Anthyllis vulneraria*. The variance in life history ratio is significant in species groups at old managed and un+new managed (high proportion of perennials), and at new managed and un+old managed (high proportion of annuals). There was no significant variation in the ratios of dispersal mode in species associated with any of the divisions of management regime.

Table 4.7 Species habits associated with management

Species solely and strongly associated with each of the management divisions and those species with no apparent association to any division, that share particular autecological habits, are presented as percentages. This demonstrates the variability of species type associated with different management regimes (Table 4.6a). The percentages of all species recorded on the bings that share the same habit are also presented. Autecological values were adapted from Hodgson et al. *(1995). Experiment-wise and comparison-wise χ^2 has been calculated between the divisions of management as described for divisions of elevation in the legend of Table 4.3. $P<0.05$ demonstrates a significant deviance from the expected in the distribution of species between the columns. Significant deviance in the proportion of species recorded at individual management divisions from the numbers recorded for all species is indicated by †.*

Habit / manag'nt	no. of spp	pH >6	pH <5	Life history annual	Life history perennial	Established strategy R*	Established strategy S*	Mode of dispersal unsp.	Mode of dispersal wind	Mode of dispersal animal
un-	28	36	11	11	89	7	21	32	50	18
old	66	†14	†18	†7	†93	†7	†35	30	36	33
new	27	33	4	†52	†48	†48	†4	30	52	18
un- +old	21	37	3	†41	†59	41	19	37	48	15
old+new	17	17	24	12	88	17	29	35	41	24
un- +new	32	52	9	†0	†100	5	14	28	48	24
no assoc'n	20	40	15	5	95	10	20	30	40	30
all species	211	37	16	22	78	24	29	30	46	24
χ^2		17.098		48.999		26.623			6.295	
p		0.009		0.000		0.000			0.900	

4.3.4 Angle of slope

Angle of slope varied within the divisions of elevation, aspect and management at all eight bing sites. Quadrats were recorded on angles of slope from 0° (flat) up to 80°, almost vertical. The quadrats were grouped by angle of slope into divisions: flat (0°), gentle slope (>0-30°) and steep slope (>30°) and the species allocated to their unique, or strongly associated, division or divisions (Table 4.8).

Table 4.8 Numbers of species and quadrats by angle of slope

The total number of quadrats and species, including cryptogams, recorded at each of the divisions of angle of slope (flat, gentle and steep) using a] the baseline data and b] the most frequent species data, are displayed. The numbers of species unique to, and strongly associated with, each division and combined division are also shown. The number of recorded quadrats is the same in both data sets. Monte Carlo analysis (Section 4.2.1) tested the significance of the number of species limited to a division or combined division by comparison with the number expected from the null model of no association between vegetation and elevation.
** highlights where the number of species unique to, or strongly associated with, a division of angle of slope is significantly ($p<0.05$) greater than the number expected.*
† highlights where the number of species unique to, or strongly associated with, a division of angle of slope is significantly ($p<0.05$) less than the number expected..

	ANGLE OF SLOPE					
	0° flat	>0-30° gentle	>30° steep	0° + >0-30°	>0-30° + >30°	0° + >30°
a] BASELINE DATA SET (211 species in 340 quadrats)						
number of quadrats	125	117	98	242	215	223
number of species recorded	164	177	144	199	196	194
unique species	15	17	12	35	†18	†7
strongly associated species	†12	†8	†5	†28	†4	†0
b] MOST FREQUENT DATA SET (104 species in 340 quadrats)						
number of species recorded	103	102	93	104	104	104
unique species	0	0	0	*11	1	2
strongly associated species	*12	6	3	†28	†4	†0

There were groups of species from the baseline data (Table 4.8a) uniquely recorded at each of the three main divisions of inclination (0°, >0-30°, >30°) but none of these were in significant numbers. The numbers of species that were unique to, and strongly associated with, the combined divisions were all significantly lower than expected however, as were the groups of species strongly associated with the main divisions.

There were no unique species from the most frequent data (table 4.8b) recorded at any of the main divisions of inclination but the group of species strongly associated with flat ground was significantly larger than expected. There was a significantly larger than expected group of species unique to the combined 0° + >0-30° division and significantly lower than expected numbers of species strongly associated with all three of the combined divisions.

The species associated with each of the divisions of inclination were linked to their expected autecological habits (Hodgson *et al.*, 1995) and dissimilarities in pH, life history, established strategy and mode of dispersal linked to angle of slope were identified (Table 4.9).

Table 4.9 Species habits associated with angle of slope

Species solely and strongly associated with each of the angle of slope divisions and those species with no apparent association to any division, that share particular autecological habits, are presented as percentages. This demonstrates the variability of species type associated with different angles of slope (Table 4.8a). The percentages of all species recorded on the bings that share the same habit are also presented. Autecological values were adapted from Hodgson et al. *(1995).*

Experiment-wise and comparison-wise χ^2 has been calculated between the divisions of angle of slope as described for divisions of elevation in the legend of Table 4.3. $P<0.05$ demonstrates a significant deviance from the expected in the distribution of species between the columns. Significant deviance in the proportion of species recorded at individual divisions from the numbers recorded for all species is indicated by †.

Habit / angle	no. of spp	pH >6	pH <5	Life history annual	Life history perennial	Established strategy R*	Established strategy S*	Mode of dispersal unsp.	Mode of dispersal wind	Mode of dispersal animal
flat	27	37	4	†48	†52	33	33	41	41	18
gentle	25	20	20	12	88	8	28	48	36	16
steep	17	24	12	6	94	6	6	24	64	12
flat/gent	63	25	11	25	75	27	29	†41	†29	†30
gent/steep	22	41	14	†0	†100	5	0	18	59	23
flat/steep	7	14	14	14	86	0	29	29	57	14
no assoc'n	50	32	14	10	90	20	22	18	52	30
all species	211	37	16	22	78	24	29	30	46	24
χ^2		4.764		27.715		5.169		21.482		
p		0.574		0.000		0.522		0.044		

The life history habit showed significant variance between annual and perennial species, and mode of dispersal, associated with divisions of angle of slope. A

significantly high proportion of annuals were recorded on flat ground and a significantly high proportion of perennials on the combined gentle+steep division. There was significant variance from all species at the flat+gentle division in the proportion of specialised wind dispersed species (lower than expected).

4.3.5 Percentage bare ground

Variation in percentage of bare ground was also within the larger scale measures of physical environment, elevation, aspect and management. Quadrats were recorded with percentages of bare ground from 0% (complete cover) to >99%. Only one of the 340 recording quadrats had 100% bare ground and no species. The quadrats were grouped into two divisions; those with 0-50% bare ground, indicating high vegetation cover, and those with >50% bare ground indicating low vegetation cover (Table 4.10).

Table 4.10 Numbers of species and quadrats by bare ground

The total number of quadrats and species, including cryptogams, recorded at each of the divisions of bare ground (high cover and low cover) using a] the baseline data and b] the most frequent species data, are displayed. The numbers of species unique to, and strongly associated with, each division are also shown. The number of recorded quadrats is the same in both data sets. Monte Carlo analysis (Section 4.2.1) tested the significance of the number of species limited to a division by comparison with the number expected from the null model of no association between vegetation and elevation.
** highlights where the number of species unique to, or strongly associated with, a division of bare ground is significantly ($p<0.05$) greater than the number expected.*
† highlights where the number of species unique to, or strongly associated with, a division of bare ground is significantly ($p<0.05$) less than the number expected.

	BARE GROUND	
	0-50% (high cover)	>50% (low cover)
a] BASELINE DATA SET (211 species in 340 quadrats)		
number of quadrats	242	98
number of species recorded	202	126
unique species	*85	9
strongly associated species	†77	22
b] MOST FREQUENT DATA SET (104 species in 340 quadrats)		
number of species recorded	104	89
unique species	*15	†0
strongly associated species	†59	†17

Significantly higher than expected numbers of unique species were recorded in quadrats with high cover in both the baseline and most frequent species data although the numbers of species strongly associated with high cover was significantly lower than expected in both data sets. There were significantly higher than expected numbers of most frequent species strongly associated to quadrats with low cover. Four of these frequent species; *Cardamine hirsuta* (11 records), *Stellaria media* (26 records), *Reseda luteola* (42 records) and *Senecio viscosus* (69 records) were strongly associated with >70% bare ground.

The groups of species associated with each of the divisions of high and low percentage of bare ground were allocated to their expected autecological habits (Hodgson *et al.*, 1995) and any relationship between pH, life history, established strategy or mode of dispersal, and ground cover were identified (Table 4.11).

Table 4.11 Species habits associated with percentage bare ground

Species solely and strongly associated with each of the percentage bare ground divisions and those species with no apparent association to either division, that share particular autecological habits, are presented as percentages. This demonstrates the variability of species type associated with different percentages of bare ground (Table 4.10a). The percentages of all species recorded on the bings that share the same habit are also presented. Autecological values were adapted from Hodgson et al. *(1995).*

Experiment-wise and comparison-wise χ^2 has been calculated between the divisions of bare ground as described for divisions of elevation in the legend of Table 4.3. $P<0.05$ demonstrates a significant deviance from the expected in the distribution of species between the columns. Significant deviance in the proportion of species recorded at individual divisions from the numbers recorded for all species is indicated by †.

Habit / cover	no. of spp	pH >6	pH <5	Life history annual	Life history perennial	Established strategy R*	Established strategy S*	Mode of dispersal unsp.	Mode of dispersal wind	Mode of dispersal animal
0-50%	162	28	15	†7	†93	†9	†26	31	42	27
>50%	31	32	0	†77	†23	†74	†3	42	52	6
no assoc'n	18	28	11	17	83	17	28	28	44	28
all species	211	37	16	22	78	24	29	30	46	24
χ^2		5.020		87.931		34.222			6.202	
p		0.081		0.000		0.000			0.185	

Life history and established strategy habits were significantly different between the two categories of percentage bare ground and also varied significantly from all

species. Species associated with high cover (0-50% bare ground) are significantly more likely to be perennial and stress tolerant and those associated with low cover (>50% bare ground) are significantly more likely to be annual and ruderal. There was no significant variance in mode of dispersal or pH although the proportion of species associated with low ground and pH <5 was significantly lower than that for all species.

4.3.6 Synthesis of plant species distributions by physical environment

Significantly more species than expected by random assortment were unique to and/or associated with measured variables in the physical environment, elevation (Table 4.2), aspect (Table 4.4), management (Table 4.6), angle of slope (Table 4.8) and bare ground (Table 4.10). A summary of the results shows that more than half of all species recorded were uniquely limited to divisions of management and elevation, almost half to divisions of angle of slope and percentage bare ground and a quarter were limited to divisions of aspect (Table 4.12). The proportion of most frequent species recorded that were limited by each of these factors was much lower but a significant 36% appeared to be limited by management.

Table 4.12 Summary table of numbers of plant species limited by physical environment

The recorded species limited by each of the measured physical environmental factors is presented as number and percentage of the full data set (211 species) and the most frequent data set (104 species)

	all species		most frequent species	
	number	%	number	%
elevation	109	52	16	15
aspect	55	26	2	2
management	138	65	37	36
angle of slope	93	44	14	13
bare ground	94	45	15	14

The variability of expected autecological habits of groups of species was significant within each of the environmental factors. Distribution of species between the divisions of elevation (Table 4.3) was linked significantly to life history (annual or perennial), mode of dispersal and pH. Distributions by aspect (Table 4.5) were linked significantly to establishment strategy (ruderal or stress tolerant) and mode of

dispersal. pH, life history and establishment strategy were significantly varied between divisions of management (Table 4.7). Significant variation was found in life history between divisions of angle of slope (Table 4.9), and in both life history and established strategy between divisions of bare ground (Table 4.11).

Each of the 104 most frequent species was strongly associated with, though not necessarily limited to, at least one of the five measured environmental factors (Table 4.13). The most widely distributed species were *Cirsium vulgare* and *Pottia davalliana*, constrained only by management and strongly associated with new managed sites, *Sambucus nigra*, constrained only by bare ground and strongly associated with more than 50% cover and *Urtica dioica*, constrained only by elevation and strongly associated with lower elevations. Twenty-five of the most frequent species were wholly limited by more than one of the measured criteria. *Calluna vulgaris* (11 quadrats), for example, was limited by all five criteria and was recorded only on old managed bings, at upper+middle elevations, with less than 30° slope, less than 50% bare ground and facing towards the cooler north and east aspects. *Polytrichum commune*, also recorded in 11 quadrats, was not wholly limited to any one division of any of the physical environmental factors, although it was strongly associated with divisions of all five criteria. *Rubus fruticosus* (16 quadrats) was also not limited, yet *R. idaeus* (17 quadrats) a closely related species with similar autecological habits, was only recorded in quadrats on the lower and middle elevations with high vegetation cover. *Tripleurospermum inodorum* (38 quadrats), *Senecio viscosus* (69 quadrats) and *Reseda luteola* (42 quadrats) were only recorded on unmanaged or newly managed sites, never on older managed sites.

Four of the most frequent species were sown during management (West Lothian Council, various dates). *Agrostis gigantea* is listed as part of a seed mix used during reclamation of Addiewell north, and *Lupinus nootkatensis*, *Poa trivialis* and *Sanguisorba minor* are listed in the seed mixes for Oakbank. *A. gigantea* (13 quadrats), *L. nootkatensis* (10 quadrats) and *P. trivialis* (16 quadrats) were only recorded in positions where they are known to be sown or planted. *S. minor* (23 quadrats) was recorded in 19 quadrats at Oakbank and also in 4 quadrats at

Addiewell south where there is no record of the species in seed mixes used during restoration of this site; because of this it is assumed to be a natural colonist.

Table 4.13 The most frequent species

Species name, number of quadrats recorded (from 340 in baseline survey), mean cover where present (as a measure of abundance) are presented with the recorded limits of measured physical environment for each of the 104 most frequent species. Autoecological information for vascular species is adapted from Hodgson et al, *(1995) with additional information from Grime* et al. *(1988) and for cryptogams has been gathered from Purvis* et al. *(1992), Smith (1978) and Smith* et al. *(2002).*
** denotes species that are listed in management plans for sites and are limited to the areas of the bings where they were seeded or planted. Lower case and italics indicate species that were strongly associated with, but not unique to, the division.*

Keys
Elevation: U = recorded only at upper elevations; U+M = recorded at upper and middle elevations but not lower elevations; L+M = recorded at lower and middle elevations but not upper elevations; U+L = recorded at upper and lower elevations but not middle elevations.
Aspect: COOL = recorded only at aspects between 315°, NW, and 134°, SE; WARM = recorded only at aspects between 135°,SE, and 314°, NW
Management: OM = recorded only on old managed sites; NM = recorded only on newly managed sites; UM = recorded only on unmanaged sites; U+O = recorded on unmanaged and old managed sites but not on newly managed sites; O+N = recorded on old and new managed sites but not unmanaged sites; U+N = recorded on unmanaged and newly managed sites but not on old managed sites.
Angle of slope: F+G = recorded at 0° (flat) and 0-30°(gentle slopes) not steep slopes; G+S = recorded at 0-30° (gentle slopes) and >30° (steep slopes) not on flat ground; F+S = recorded at 0° (flat) and >30° (steep slopes) not on gentle slopes
Bare ground: 0-50% = recorded with high vegetation cover
Soil pH: The numeral indicates the modal pH class for the species followed by a letter indicating the number of pH classes in which the frequency of the species exceeds 50% of that in its modal class. Thus 5a indicates that the species is most frequent within the range 5-5.9 and has a range of only 1 pH unit. In contrast 4d indicates a mode within the interval pH 4-4.9 and a range of 4 pH units.
Life history: P = perennial; A = annual; B = biennial.
Established (est.) strategy: allocation to C-S-R (competitive, stress-tolerant or ruderal) strategies as described in Chapter Three, Section 3.1.4. Besides the three primary strategies (C, S and R) there are four secondary strategies (CR, SC, SR and CSR) and twelve tertiary strategy types (e.g. CR/CSR and R/SR) making a total of nineteen functional types in all.
Agency of (propagule) dispersal: WINDp = wind dispersed, dispersule plumed or wrapped in hairs; WINDw = seeds winged or flattened; WINDc = seeds small/minute and shed from a capsule; ANIMa = animal dispersed, dispersule with awn; ANIMb = animal dispersed, dispersule an adhesive burr; ANIMi = dispersed, ingested berry; ANIMe = animal dispersed, seed dispersed by ants; UNSP = unspecialised; UNSPag = unspecialised but dispersed widely as a result of agricultural practices; AQUAT = dispersed by water

species	number of quadrats	% mean cover where present	elevation	aspect	manage-ment	angle of slope	bare ground	pH	life form	est. strategy	agency of dispersal
Acer pseudoplatanus	9	1.44	L+M	*warm*	U+O	>0-30+>30	*0-50%*	7e	P	C/SC	WINDw
Achillea millefolium	10	6.90	L+M	-	U+N	*0+>0-30*	0-50%	5c	P	CR/CSR	WINDw
*Agrostis gigantea**	13	11.54	U	-	OM	0+>0-30	0-50%	6c	P	CR	UNSP
Alliaria petiolata	9	2.33	*l*	*cool*	U+N	*0*	-	6b	P	CR	UNSP
*Alnus glutinosa**	16	1.75	L+M	-	OM	0+>0-30	*0-50%*	6d	P	SC	WINDw
Angelica sylvestris	11	9.27	*m*	*cool*	U+O	*>0-30+>30*	0-50%	5d	P	C/CR	AQUAT
Anthoxanthum odoratum	15	7.73	*l*	*cool*	*u+n*	*0*	*0-50%*	5b	P	SR/CSR	ANIMa
Anthriscus sylvestris	20	2.90	*l*	*cool*	*u+o*	*>0-30+>30*	*0-50%*	7c	P	CR	UNSP
Arctium minus	13	11.62	*l*	*cool*	U+N	*>30*	*0-50%*	7a	P	CR	ANIMb
Arenaria serpyllifolia	21	1.95	*u*	-	U+N	*0*	-	7a	A	SR	WINDc
Arrhenatherum elatius	133	15.42	*u+l*	-	-	-	*0-50%*	7c	P	C/CSR	ANIMa
Bellis perennis	9	3.22	*u+l*	*cool*	-	*0+>0-30*	*0-50%*	7c	P	R/CSR	UNSP
Betula pendula	63	7.86	*l*	-	-	-	*0-50%*	3b	P	C/SC	WINDw
Bryum pallens	12	2.75	L+M	-	U+N	*>0-30*	*0-50%*	basic	P	-	WINDc
Calluna vulgaris	11	37.36	U+M	COOL	OM	0+>0-30	0-50%	3a	P	SC	WINDc
Cardamine hirsuta	11	1.00	*u*	-	U+N	0+>30	*>50%*	7a	A	SR	WINDw
Centaurea nigra	81	10.07	*u+l*	-	*u+o*	-	*0-50%*	7c	P	CSR	UNSP
Cerastium fontanum	84	2.15	-	-	-	*0*	*0-50%*	5c	P	R/CSR	UNSP
Cerastium glomeratum	15	1.53	*m*	-	NM	*0*	*>50%*	7c	A	R/SR	WINDc
Chamerion angustifolium	141	8.45	*l*	-	-	-	*0-50%*	4d	P	C	WINDp
Chenopodium album	11	1.36	-	-	O+N	*0*	*>50%*	6c	A	R/CR	UNSP
Cirsium arvense	108	5.59	*l*	-	*nm*	-	*0-50%*	5c	P	C	WINDp
Cirsium vulgare	41	1.68	-	-	*nm*	-	-	5c	P	CR	WINDp
Cladonia fimbriata	25	4.44	*l*	-	*um*	-	*0-50%*	-	P	-	WIND
Crataegus monogyna	39	4.77	*u+l*	-	*o+n*	-	*0-50%*	7c	P	SC	ANIMi
Cynosurus cristatus	13	6.77	*u*	-	U+O	*0+>0-30*	0-50%	6c	P	CSR	UNSPag
Cytisus scoparius	38	8.79	*l+m*	-	*om*	*0+>0-30*	*0-50%*	4c	P	SC	ANIMe
Dactylis glomerata	79	9.01	*u+l*	-	-	*0+>0-30*	*0-50%*	7c	P	C/CSR	UNSPag
Dactylorhiza fuchsii	31	1.42	*u+l*	-	O+N	*0+>0-30*	0-50%	7c	P	S/CSR	WINDc
Deschampsia cespitosa	37	17.59	*l*	*cool*	-	*0+>0-30*	*0-50%*	5c	P	SC/CSR	ANIMa
Deschampsia flexuosa	123	39.05	-	-	*om*	*0+>0-30*	*0-50%*	3a	P	S/SC	ANIMa
Epilobium hirsutum	14	6.43	L+M	-	*u+n*	0+>0-30	-	7b	P	C	WINDp
Epilobium montanum	60	1.88	*l+m*	-	*nm*	-	*0-50%*	7c	P	CSR	WINDp
Euphrasia nemorosa	53	3.53	*u+l*	-	-	*0+>0-30*	*0-50%*	7b	A	SR	WINDc
Festuca ovina	79	15.47	*u*	-	U+N	-	-	W3	P	S	ANIMa
Fragaria vesca	21	20.00	*u+l*	-	*u+o*	*0+>0-30*	*0-50%*	7a	P	CSR	ANIMi
Galeopsis tetrahit	9	1.00	-	-	NM	0+>0-30	*>50%*	6b	A	R/CR	UNSPag
Galium aparine	27	6.26	*l+m*	*warm*	*om*	*0+>0-30*	*0-50%*	7c	A	CR	ANIMb
Heracleum sphondylium	52	4.67	*u+l*	-	*um*	-	*0-50%*	5c	P	CR	WINDw
Holcus lanatus	182	21.08	*u+l*	-	*u+o*	*0+>0-30*	*0-50%*	5c	P	CSR	UNSP
Holcus mollis	45	10.89	*l+m*	-	*o+n*	*>0-30+>30*	*0-50%*	4b	P	C/CSR	ANIMa
Hypnum cupressiforme	113	24.11	*u+l*	*cool*	-	-	*0-50%*	wide	P	-	WINDc
Hypochoeris radicata	61	3.18	*u+l*	-	-	-	*0-50%*	5b	P	CSR	WINDp
Lathyrus pratensis	42	7.45	*l*	-	*om*	*0+>0-30*	*0-50%*	5c	P	CSR	UNSP
Leucanthemum vulgare	124	8.39	*u+l*	-	-	-	*0-50%*	7a	P	C/CSR	UNSPag
Linaria vulgaris	24	5.00	*l+m*	*cool*	*nm*	*>30*	*0-50%*	6c	P	CR	WINDc
Linum catharticum	22	1.95	U+L	*cool*	*um*	*0*	*0-50%*	7a	A	SR	UNSP
Lophocolea cuspidata	64	27.14	*l*	*cool*	*om*	*0+>0-30*	*0-50%*	-	P	-	WIND
Lotus corniculatus	15	12.20	*u+l*	*cool*	-	*0*	0-50%	7c	P	S/CSR	UNSP
*Lupinus nootkatensis**	10	10.60	*u*	-	OM	*>0-30*	0-50%	-	P	C	ANIM
Luzula multiflora	9	3.33	U+L	*cool*	*o+n*	0+>30	*0-50%*	4d	P	S	ANIMe
Matricaria discoides	15	1.27	*u+m*	*warm*	NM	0+>0-30	*>50%*	7c	A	R	UNSP
Medicago lupulina	40	11.85	*l*	-	*u+n*	*0+>0-30*	*0-50%*	7a	A	R/SR	UNSP
Myosotis arvensis	66	2.39	*u*	-	*nm*	-	*>50%*	6b	A	R/SR	ANIMa
Odontites verna	25	2.68	*l*	*cool*	*u+n*	*0+>0-30*	*0-50%*	7c	A	R	WINDc
Papaver dubium	9	1.89	*l+m*	*cool*	U+N	*0*	*>50%*	6c	A	R	WINDc
Peltigera canina	12	6.00	*m*	COOL	U+O	*>0-30+>30*	*0-50%*	-	P	-	WIND
Pilosella officinarum	32	4.84	*u+l*	-	*u+n*	-	-	7c	P	S/CSR	WINDp
Plantago lanceolata	104	7.85	*u+l*	-	*u+o*	-	*0-50%*	7c	P	CSR	ANIMm
Plantago major	10	2.20	*l*	-	U+N	0+>0-30	*0-50%*	7b	P	R/CSR	ANIMm
Poa annua	11	7.91	*u*	-	O+N	*0*	*0-50%*	7c	A	R	UNSPag

species	number of quadrats	mean cover where present	elevation	aspect	manage-ment	angle of slope	bare ground	pH	life form	est. strategy	agency of dispersal
Poa nemoralis	28	10.29	L+M	-	*o+n*	*0+>0-30*	*0-50%*	6d	P	S/CSR	UNSP
*Poa trivialis**	16	20.31	*u*	-	OM	*>0-30*	0-50%	7c	P	CR/CSR	UNSPag
Polygonum aviculare	19	1.21	*m*	-	U+N	*0+>0-30*	*>50%*	6c	A	R	UNSPag
Polygonum maculosa	19	1.42	*u+m*	-	U+N	*0+>0-30*	*>50%*	5b	A	R	UNSPag
Polytrichum commune	11	16.45	*u+l*	*cool*	*om*	*0*	*0-50%*	acid	P	-	WINDc
Polytrichum juniperum	19	15.53	-	-	*um*	*>30*	-	acid	P	-	WINDc
Potentilla erecta	10	7.70	*u*	-	OM	0+>0-30	0-50%	4b	P	S/CSR	UNSP
Pottia davalliana	9	7.22	-	-	*nm*	-	-	basic	P	-	WINDc
Prunella vulgaris	29	2.72	*u+l*	-	*om*	-	*0-50%*	5a	P	CSR	ANIMm
Ranunculus acris	19	1.84	U+M	-	O+N	*0+>0-30*	0-50%	6c	P	CSR	ANIMa
Ranunculus repens	89	7.99	*l*	-	-	-	*0-50%*	6c	P	CR	ANIMa
Reseda luteola	42	3.76	*u+m*	-	U+N	-	*>50%*	6b	B	R/CSR	WINDc
Rhinanthus minor	28	2.54	*u*	-	*om*	0+>0-30	0-50%	5b	A	R/SR	WINDc
Rhytidiadelphus squarrosus	45	29.47	*u+l*	*cool*	*om*	-	0-50%	-	P	-	WINDc
Rosa canina agg.	17	1.94	*l*	-	*um*	-	*0-50%*	7b	P	SC	ANIMi
Rubus fruticosus agg.	16	10.94	*l*	-	*um*	*0*	*0-50%*	4b	P	SC	ANIMi
Rubus idaeus	17	28.53	L+M	-	-	-	0-50%	4d	P	SC	ANIMi
Rumex acetosa	28	4.36	*u*	-	*om*	*0+>0-30*	*0-50%*	5c	P	CSR	WINDw
Rumex acetosella	17	4.00	*l*	-	U+O	-	-	4c	P	SR/CSR	UNSP
Rumex crispus	20	2.90	*u+l*	-	*u+n*	*0+>0-30*	-	6b	P	R/CR	UNSP
Rumex obtusifolius	26	4.08	*l+m*	-	*nm*	*0+>0-30*	-	7c	P	CR	ANIMa
Sagina procumbens	27	4.41	*u*	-	*nm*	-	*>50%*	5c	P	R/CSR	UNSPc
Salix caprea	33	4.15	*l*	*cool*	-	-	*0-50%*	6a	P	C	WINDp
Sambucus nigra	11	3.45	-	-	-	-	*0-50%*	5c	P	C	ANIMi
*Sanguisorba minor**	23	8.52	*u*	-	OM	-	0-50%	5c	P	S	UNSP
Senecio jacobaea	77	2.65	-	-	*um*	-	*0-50%*	7a	P	R/CR	WINDp
Senecio viscosus	69	5.28	*u+m*	-	U+N	-	*>50%*	7c	A	R	WINDp
Senecio vulgaris	23	2.04	*u+m*	-	U+N	*0+>0-30*	*>50%*	7a	A	R	WINDp
Sonchus asper	28	1.57	*m*	-	*nm*	-	*>50%*	7c	A	R/CR	WINDp
Sorbus aucuparia	13	2.31	L+M	-	*om*	*0+>0-30*	*0-50%*	3a	P	SC	ANIMi
Stellaria media	26	3.04	*u*	-	NM	0+>0-30	*>50%*	6c	A	R	UNSPag
Taraxacum officinale agg.	34	2.32	*l*	*cool*	*o+n*	-	*0-50%*	7b	P	R/CSR	WINDp
Trifolium campestre	46	6.74	*u+l*	-	*um*	*0*	*0-50%*	6c	A	SR	ANIMa
Trifolium pratense	29	12.21	*u*	-	*om*	*0+>0-30*	*0-50%*	5c	P	CSR	ANIMa
Trifolium repens	115	14.14	*u+l*	-	-	*0+>0-30*	*0-50%*	5c	P	CR/CSR	ANIMa
Tripleurospermum inodorum	38	5.03	*l+m*	-	U+N	*0+>0-30*	-	6c	A	R	UNSPag
Tussilago farfara	89	6.45	*l*	-	-	-	*0-50%*	7b	P	CR	WINDp
Urtica dioica	37	3.81	*l*	-	-	-	-	6c	P	C	ANIMa
Veronica persica	9	1.89	*u*	*cool*	U+N	0+>0-30	*>50%*	6b	A	R	UNSPag
Veronica serpyllifolia	15	1.53	*u+m*	-	U+N	-	*>50%*	6c	P	R/CSR	UNSP
Vicia cracca	19	5.53	L+M	-	*om*	*>0-30*	*0-50%*	6b	P	C/CSR	UNSP
Vicia hirsuta	34	5.74	*l*	-	*om*	-	*0-50%*	6c	A	R/CSR	UNSP
Vicia sativa	10	1.40	L+M	-	*om*	*>0-30*	*0-50%*	6d	A	R/CSR	UNSP

There was considerable variation in the abundance of the different species in this data set, although they were recorded in the highest numbers of quadrats (i.e.most frequently). Five species were all recorded at a mean of over 25% quadrat cover; *Calluna vulgaris* (11 quadrats), *Deschampsia flexuosa* (123 quadrats), *Lophocolea cuspidata* (64 quadrats), *Rhytidiadelphus squarrosus* (45 quadrats) and *Rubus idaeus* (17 quadrats). Yet *Galeopsis tetrahit* (9 quadrats) and *Cardamine hirsuta* (11 quadrats) were only ever recorded at 1% cover. Perennial species were generally more abundant than annuals, measured as mean cover where present. However, the

annual species *Galium aparine* (27 quadrats), *Medicago lupulina* (40 quadrats), *Poa annua*, (11 quadrats), *Senecio viscosus* (69 quadrats), *Trifolium campestre* (46 quadrats), *Tripleurospermum inodorum* (38 quadrats) and *Vicia hirsuta* (34 quadrats) were all consistently recorded at more than 5% cover. The mean cover where present of *M. lupulina*, the most abundant of the annual species, was 11.85%. Nine of the most frequently recorded species were cryptogams: six mosses, two lichens and a leafy liverwort. The abundance of two of these, *L. cuspidata* and *R. squarrosus*, has already been noted. The others were *Bryum pallens, Cladonia fimbriata, Hypnum cupressiforme, Peltigera canina, Polytrichum commune, P. juniperum* and *Pottia davalliana.* Cryptogams covered a total of 21% of the substrate in the 340 quadrats recorded in the baseline survey (286 m^2 out of 1360 m^2 surveyed). The greatest contributors were *H. cupressiforme* (24% cover in 113 quadrats), *L. cuspidata* (27% cover in 64 quadrats) and *R. squarrosus* (29% cover in 45 quadrats).

4.4 Chemical Analysis and Nutrient Distribution

Chemical analysis of the substrate (described in section 4.2.2) revealed the extent of variation in soil nutrients and pH both within and between bing sites. There was no statistically significant difference (Wilcoxon Ranked Sign Test) between the measurements of sodium and phosphorus in the pairs of subsoil and surface samples taken from each quadrat. The measurements of potassium, sodium, nitrate and pH between the pairs of surface and subsoil samples were similar (although not statistically significant, correlations were all above 75%) but those for magnesium and ammonia showed less than 30% correlation between paired measurements. A summary of the minimum and maximum measurements of calcium, sodium, phosphorus, potassium, magnesium, available nitrogen (nitrate and ammonia) and pH for each of the four sites sampled is presented in Table 4.14.

Nitrogen availability was not measured in the substrate samples from Greendykes and Mid Breich due to problems during storage. A complete table of results is presented in Appendix 13. The measured nutrients were repeatedly recorded at levels that would be expected to cause problems relating to toxicity (high levels) or

deficiency (low levels), or both, in many plant species. Measurements of potassium, phosphorus, calcium and nitrogen that were outside the expected optimum requirements for normal plant growth (Bradshaw and Chadwick, 1980; Agvise Laboratories, undated) were each recorded in more than 40% of the samples. Calcium, for example, was measured from one tenth of the minimum to ten times the maximum requirements and fewer than 10% of samples contained even the minimum requirement of available nitrogen.

Table 4.14 Summary of results from chemical analyses

The minimum and maximum measurements, median and interquartile ranges of pH, sodium and the five macronutrients, in parts per million, from the four sample sites are compared with the minimum and maximum requirements for optimum plant growth (Bradshaw and Chadwick, 1980; Agvise Laboratories, undated). The numbers of samples with measurements that are above and below the optimal range are also shown. There were 100 soil samples (50 surface and 50 subsoil) analysed for Na, Mg, K, P, Ca and pH. Forty-eight samples (24 surface and 24 subsoil) were analysed for NH_4^+ and NO_3^-.

	Na	Mg	K	P	Ca	pH	NH_4^+	NO_3^-
minimum	1	16	5	5	50	5.72	0.05	0.03
Q1	23	102	75	10	1194	6.28	0.08	0.39
median	32	213	123	18	1900	6.69	0.10	0.62
Q2	44	327	221	31	3573	7.29	0.13	1.05
maximum	275	1289	371	180	20300	8.17	0.47	4.67
optimum min	0	50	100	5	500	5.00	2	2
optimum max	120	300	300	20	2000	7.50	20	20
no. of samples below opt. range	0	10	41	1	10	0	48	43
no. of samples above opt. range	2	29	6	47	48	22	0	0

The extent of the variation between the four bing sites is exemplified using potassium, phosphorus and pH (Figure 4.2). Potassium (Figure 4.2a) was recorded mainly within Bradshaw and Chadwick's (1980) optimal requirements of between 100 and 300 ppm at both Greendykes and Oakbank. At Mid Breich half of the samples were below the optimum, the lowest recording was 49 ppm, and at Clapperton only the three highest measurements reached optimum levels, the bulk of samples (58%) contained less than 50 ppm. Samples from Greendykes had the widest range of variability (55-370 ppm) and Clapperton the narrowest range (5-120 ppm).

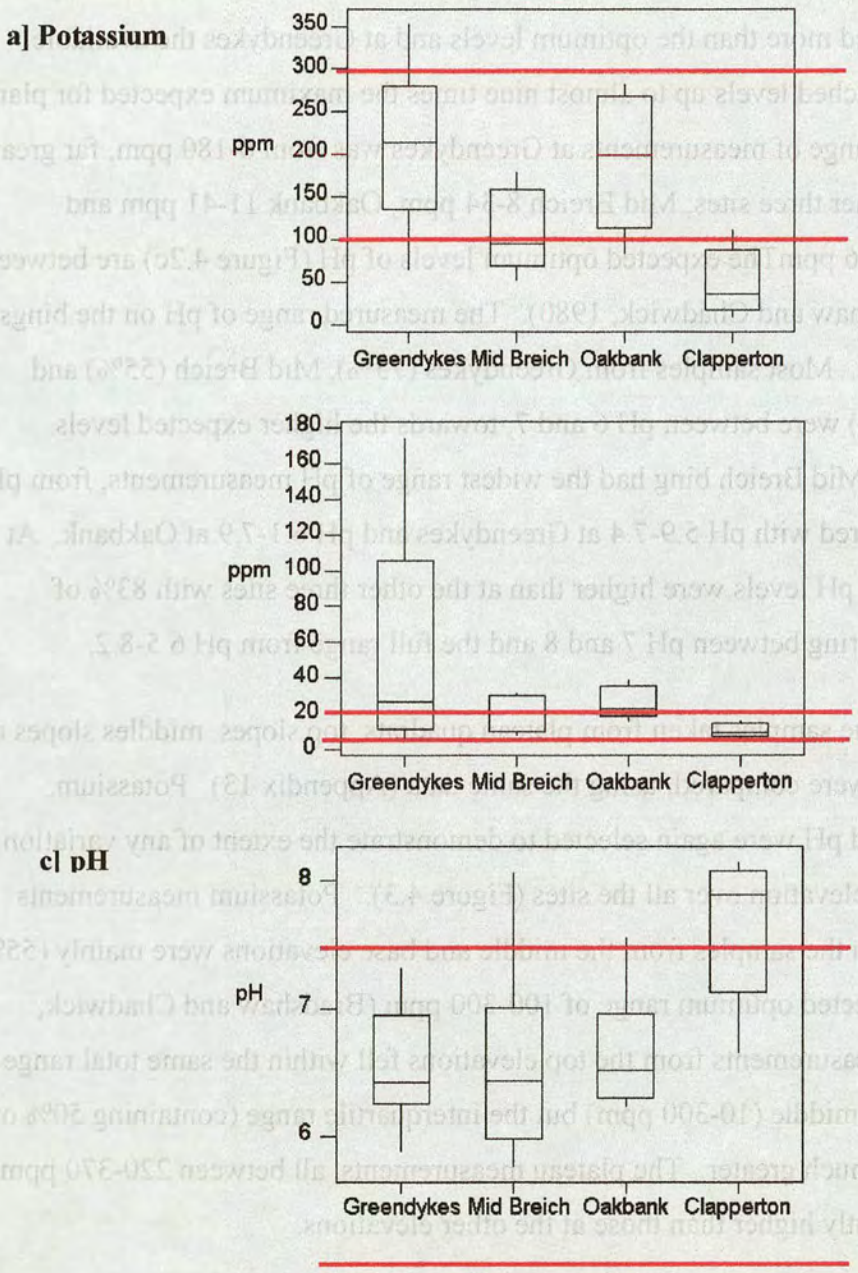


Figure 4.2 Variation in nutrients between and within bing sites

Measured potassium, phosphorus and pH at Greendykes (32 samples), Mid Breich (20 samples), Oakbank and Clapperton (24 samples each) are displayed as boxplots, showing median, interquartile range and over all range, to demonstrate the variation between and within the sites. The bold parallel lines mark the expected minimum and maximum values for optimum plant growth (Bradshaw and Chadwick, 1980).

Phosphorus (Figure 4.2b) was recorded wholly within the optimum levels, between 5 and 20 ppm (Bradshaw and Chadwick, 1980), at Clapperton but only the lower 45%

of values at Mid Breich came within this range. At Oakbank most of the samples (79%) contained more than the optimum levels and at Greendykes the available phosphorus reached levels up to almost nine times the maximum expected for plant growth. The range of measurements at Greendykes was from 6-180 ppm, far greater than for the other three sites; Mid Breich 8-34 ppm, Oakbank 11-41 ppm and Clapperton 5-16 ppmThe expected optimum levels of pH (Figure 4.2c) are between 5 and 7.5 (Bradshaw and Chadwick, 1980). The measured range of pH on the bings was pH 5.7-8.2. Most samples from Greendykes (75%), Mid Breich (55%) and Oakbank (79%) were between pH 6 and 7, towards the higher expected levels. Samples from Mid Breich bing had the widest range of pH measurements, from pH 5.7- 8.1 compared with pH 5.9-7.4 at Greendykes and pH 6.1-7.9 at Oakbank. At Clapperton the pH levels were higher than at the other three sites with 83% of samples measuring between pH 7 and 8 and the full range from pH 6.5-8.2.

Results from the samples taken from plateau quadrats, top slopes, middles slopes and base quadrats were compared, using the same data (Appendix 13). Potassium, phosphorus and pH were again selected to demonstrate the extent of any variation in nutrients with elevation over all the sites (Figure 4.3). Potassium measurements (Figure 4.3a) in the samples from the middle and base elevations were mainly (55%) within the expected optimum range of 100-300 ppm (Bradshaw and Chadwick, 1980). The measurements from the top elevations fell within the same total range as those from the middle (10-300 ppm) but the interquartile range (containing 50% of the data) was much greater. The plateau measurements, all between 220-370 ppm, were significantly higher than those at the other elevations.

The amount of phosphorus measured in samples from each of the elevations was also varied (Figure 4.3b). The plateau samples were all within the expected optimum range for plant growth of 5-20 ppm (Bradshaw and Chadwick, 1980) as were 50% of the top middle and base samples. However although the top and middle samples have a similar overall range between 5 and 50 ppm (with the exception of one very high outlying reading of 130 ppm from a middle sample) the base samples were measured between 7 and 180 ppm.

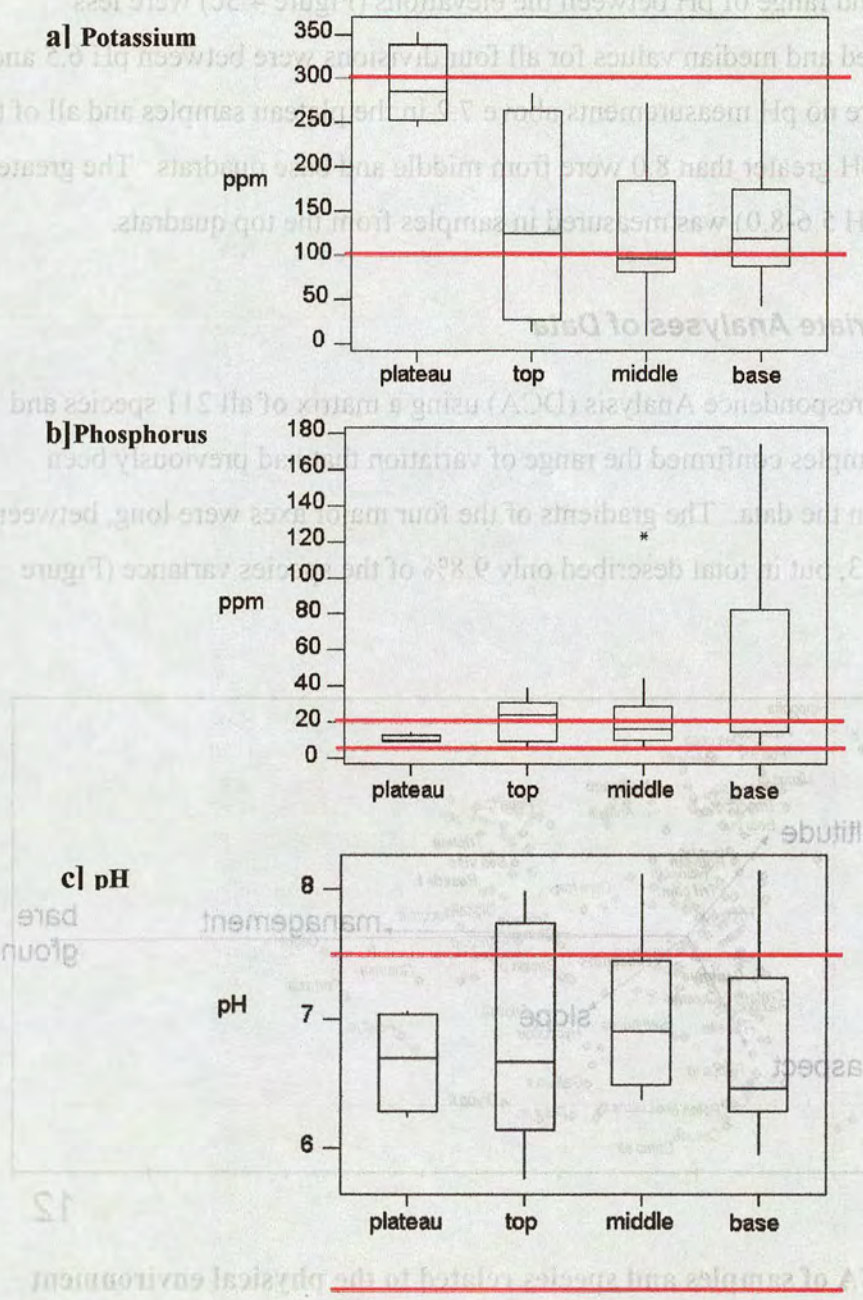


Figure 4.3 Variation in nutrients between positions

Measurements of potassium, phosphorus and pH at each of the four positions (plateau,8 samples; top, 28 samples; middle and base, 32 samples each) are displayed as boxplots, showing median, interquartile range and over all range, to show the extent that the variation within the sites correlates with elevation. The bold parallel lines mark the expected minimum and maximum values for optimum plant growth (Bradshaw and Chadwick, 1980). The asterisk (*) on Figure 4.3b] identifies an outlier in the data; a single measurement with a value lying between 1.5 and 3 times away from the middle 50% of the data (Minitab, Inc., 2000).

The measure and range of pH between the elevations (Figure 4.3c) were less obviously varied and median values for all four divisions were between pH 6.5 and 6.9. There were no pH measurements above 7.2 in the plateau samples and all of the samples with pH greater than 8.0 were from middle and base quadrats. The greatest range of pH (pH 5.6-8.0) was measured in samples from the top quadrats.

4.5 Multivariate Analyses of Data

Detrended Correspondence Analysis (DCA) using a matrix of all 211 species and 340 quadrat samples confirmed the range of variation that had previously been observed within the data. The gradients of the four major axes were long, between 7.184 and 3.713, but in total described only 9.8% of the species variance (Figure 4.4).

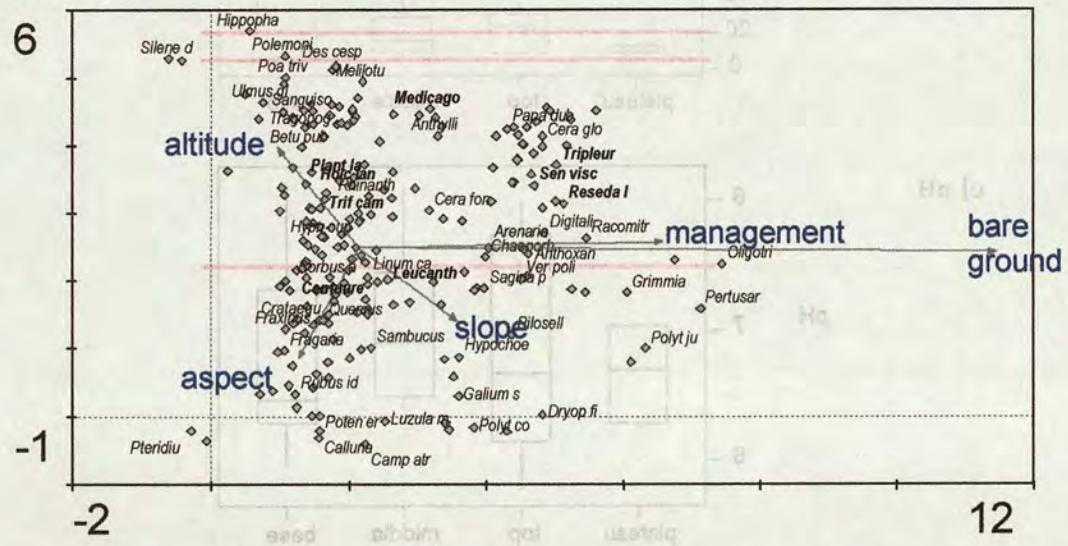


Figure 4.4 DCA of samples and species related to the physical environment

The distribution of species along the first two ordination gradients in DCA analysis produced in CANODRAW as a triplot with environmental axes superimposed as supplementary data. A few species names have been retained to indicate possible associations. The species in bold are nine named species whose relationship is discussed in the text and are highlighted in figures 4.6 and 4.8.

When measured physical environmental gradients (elevation, aspect, slope, bare ground and management) were superimposed over the DCA scatter plot, as supplementary data, 79% of described variation on the first ordination axis corresponded to bare ground. A similar result was calculated using the most frequent

species data: 13.85% of the species variance was described in total by the first four axes and 77% of the first ordination axis corresponded to bare ground.

4.5.1 Analysis of the effect of physical environment

Canonical Correspondence analysis (CCA) of the same data sets demonstrated that the first four constrained axes (measured physical environmental variables) accounted for a total of 94% of the 13.85% described variance in the DCA for the most frequent species and 93% of the 9.8% variance described in the DCA for all species. The environmental axes of bare ground and management are no longer describing the same ordination axis (as in DCA) but are correlated with the two main canonical axes of variance (Figure 4.5). The overall pattern of species has been tilted slightly and stretched along the bare ground axis.

This analysis clearly separates the 15 frequently recorded species that were associated with bare ground (Table 4.10) into a cluster (enclosed in the solid circle at the top right hand corner of Figure 4.5) and includes the four species that were strongly associated with 70% bare ground. These were *Cardamine hirsuta*, *Stellaria media*, *Reseda luteola* (enclosed in solid rectangle) and *Senecio viscosus* (enclosed in solid rectangle). The species associated with high cover (0-50% bare ground) are indiscernible from the larger body of species grouped in the top left of the plot (enclosed in a broken circle on Figure 4.5).

Individual species indicated on the plot (Figure 4.5) are those that had been identified as having recognisable distribution patterns from observations in the field. *Reseda luteola* and *Senecio viscosus* grew together in similar habitats on the bing sites but were rarely seen in the surrounding landscape. *Medicago lupulina* and *Trifolium campestre* (Fabaceae), and *Leucanthemum vulgare* and *Tripleurospermum inodorum* (Asteraceae) are closely related pairs of species (indicated by solid rectangles linked with arrows). Each pair of species shares ecological habits and gave the impression of growing in similar habitats in the field, but were rarely recorded together on any site. *Holcus lanatus*, *Centaurea nigra* and *Plantago lanceolata* were frequently recorded species that appeared on all of the bing sites and were also common to many local habitats within West Lothian (enclosed in broken rectangle).

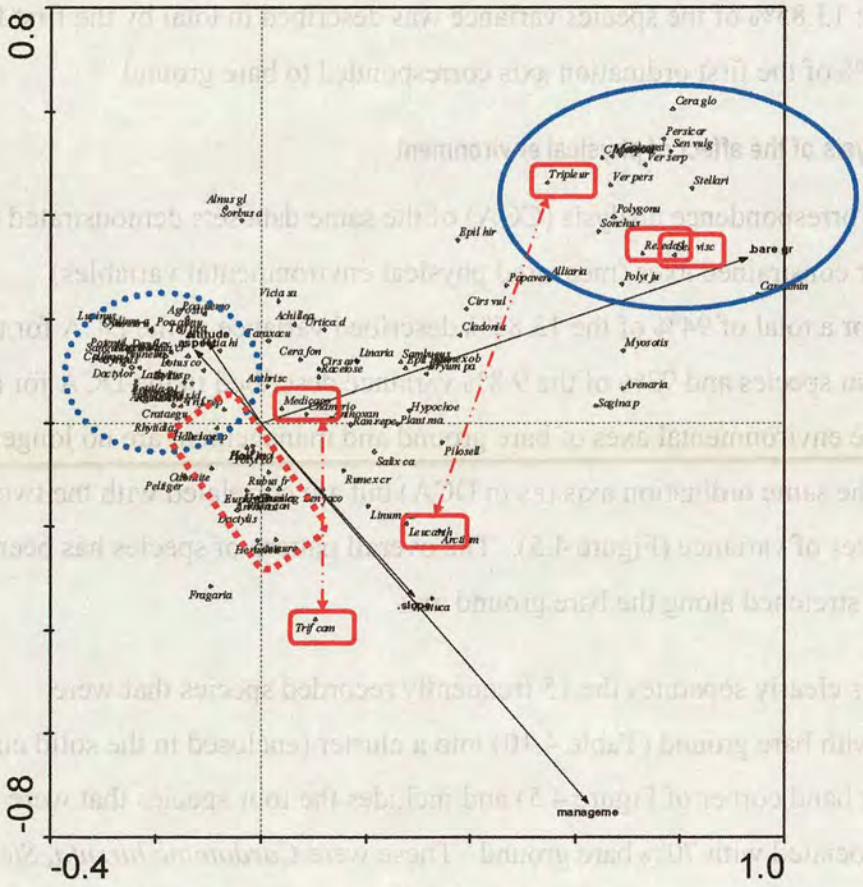


Figure 4.5 CCA of samples, the top 100 species and physical environment

The cluster of species circled with a solid line at the top right hand side of the diagram contains the15 species unique to quadrats with more than 50% bare ground (Table 4.10). The broken circle on the left encloses the species associated only with dense vegetation but groups them with many other species. The individual species enclosed in solid rectangles are Reseda luteola *and* Senecio viscosus. *The paired species, linked by arrows, are* Medicago lupulina *and* Trifolium campestre, *and* Leucanthemum vulgare *and* Tripleurospermum inodorum. *The broken rectangle encloses a group containing* Holcus lanatus, Centaurea nigra *and* Plantago lanceolata. *The relevance of these species is discussed in the text.*

When CCA was carried out on the full data set species associated with the three management regimes could clearly be seen grouped in different positions along the axes corresponding with management (Figure 4.6). The less commonly recorded species associated with the three different management regimes now clearly separate the groups along the management axis with old managed at the top, new managed in the middle and unmanaged at the bottom (enclosed by dotted lines). Each group of species is also clearly influenced by bare ground.

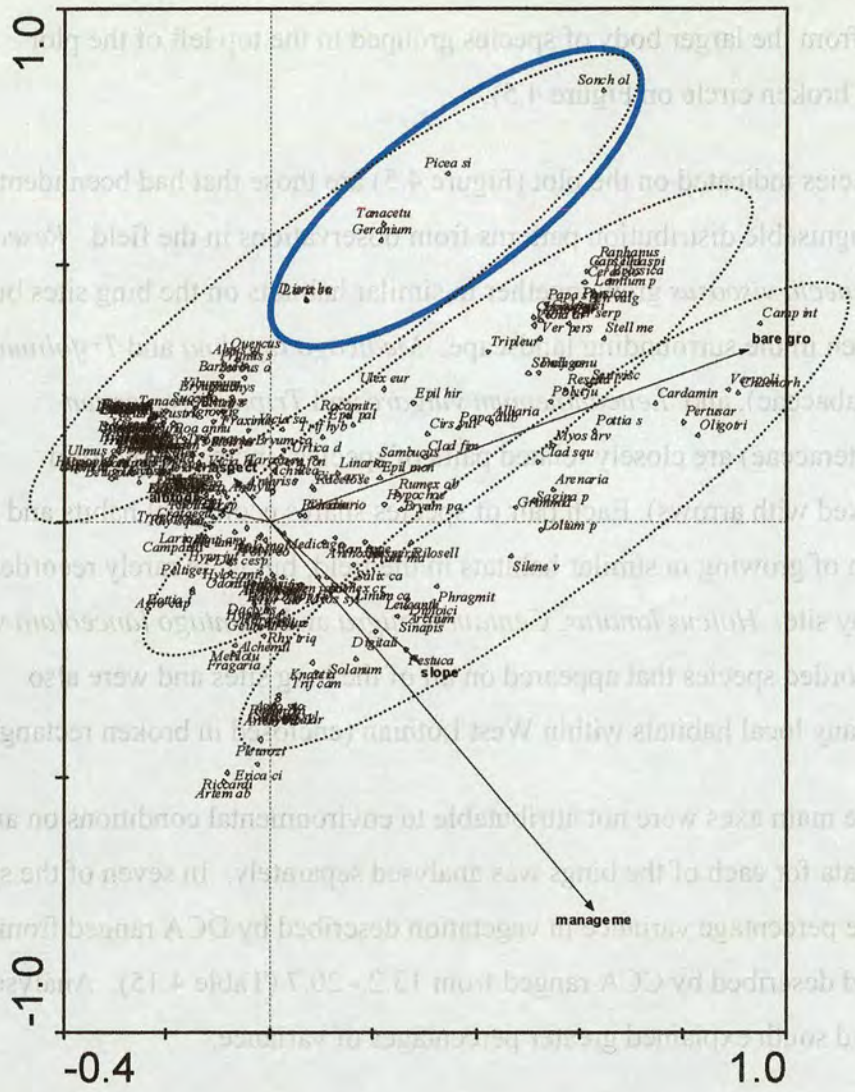


Figure 4.6 CCA of samples, all 211 species and physical environment

The effect of including the uncommon species to the CCA can be seen in the continuation of the group that had truncated at Alnus glutinosa *in Figure 4.5 but now extends to the top right of the diagram (circled with a solid line). The species associated with the three different management regimes are clearly separated along the management axis with old managed at the top, new managed in the middle and unmanaged at the bottom (enclosed by dotted lines).*

This analysis clearly separates the 15 frequently recorded species that were associated with bare ground (Table 4.10) into a cluster (enclosed in the solid circle at the top right hand corner of Figure 4.5) and includes the four species that were strongly associated with 70% bare ground. These were *Cardamine hirsuta, Stellaria media, Reseda luteola* (enclosed in solid rectangle) and *Senecio viscosus* (enclosed in solid rectangle). The species associated with high cover (0-50% bare ground) are

indiscernible from the larger body of species grouped in the top left of the plot (enclosed in a broken circle on Figure 4.5).

Individual species indicated on the plot (Figure 4.5) are those that had been identified as having recognisable distribution patterns from observations in the field. *Reseda luteola* and *Senecio viscosus* grew together in similar habitats on the bing sites but were rarely seen in the surrounding landscape. *Medicago lupulina* and *Trifolium campestre* (Fabaceae), and *Leucanthemum vulgare* and *Tripleurospermum inodorum* (Asteraceae) are closely related pairs of species (indicated by solid rectangles linked with arrows). Each pair of species shares ecological habits and gave the impression of growing in similar habitats in the field, but were rarely recorded together on any site. *Holcus lanatus*, *Centaurea nigra* and *Plantago lanceolata* were frequently recorded species that appeared on all of the bing sites and were also common to many local habitats within West Lothian (enclosed in broken rectangle).

To test that the main axes were not attributable to environmental conditions on any one site, the data for each of the bings was analysed separately. In seven of the sites the cumulative percentage variance in vegetation described by DCA ranged from 22.3 - 27.5 and described by CCA ranged from 13.2 - 20.7 (Table 4.15). Analyses of Drumshoreland south explained greater percentages of variance.

Table 4.15 Analysis of physical environment on individual bings

The cumulative percentage variation (cum. var.) in species described by the first four axes in DCA and CCA for the eight bings is presented with the main contributing measured physical environmental factors to the first CCA axis in each site.

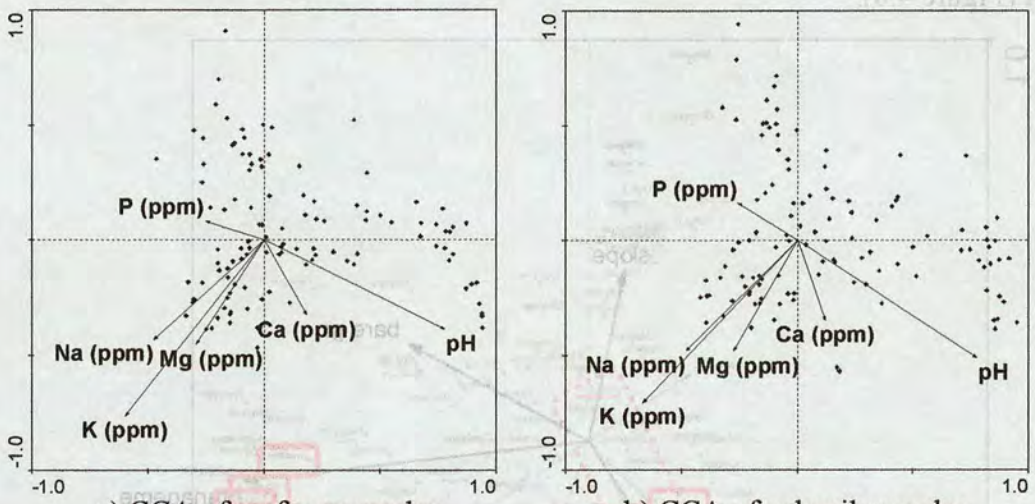
Bing site	DCA cum. var.	CCA cum. var.	First axis
Addiewell north	23.6	13.6	Position (0.86)
Addiewell south	25.1	15.0	Position (0.71)
Clapperton	22.3	18.6	Bare ground (0.91)
Drumshoreland north	27.5	20.7	Bare ground (0.91)
Drumshoreland south	40.3	57.5	Bare ground (0.98)
Greendykes	24.7	13.2	Bare ground (0.59)
			Position (-0.53)
Mid Breich	26.1	15.9	Bare ground (0.89)
Oakbank	25.0	19.9	Position (-0.90)

At four of the eight sites the explained variation on the first canonical axis correlated strongly with bare ground and on three sites, with position (as a measure of

elevation). At Greendykes the explained variation correlated equally with these two environmental axes. The environmental effects of slope and management were less strongly correlated with minor axes at all eight sites.

4.5.2 Analysis of the effect of the chemical environment

The samples and species were associated with the chemical environment in two smaller data sets (surface soil and subsoil) based on 50 quadrats from four bing sites as described in Section 4.2. These were analysed individually using CCA (Figure 4.7) because of the variation that had been measured in the soil chemistry between the surface and sub-soil samples (Section 4.4 and Appendix 13).



a) CCA of surface samples b) CCA of subsoil samples

Figure 4.7 CCA of samples, species and the surface and subsoil chemistry

This pair of diagrams produced in CANODRAW demonstrates the similarity of distribution of species in relation to soil chemistry gradients between the surface soil samples and the subsoil samples.

The gradients of pH and phosphorus are represented at opposite ends of the same axis showing that they are negatively correlated with each other. Three of the remaining nutrients, sodium, potassium and magnesium, are represented by axes aligned vertically to the pH/phosphorus axis with the gradients running in the same direction. The calcium axis is positioned midway between these and pH. Only a small amount of the cumulative percentage variance of species was explained by the soil nutrients (14% of surface samples and 13% of subsoil samples). Both pH and

potassium have long gradients and in the CCAs the first axes corresponded with pH (correlation was 0.70 for both surface and sub-soil) and the second axes corresponded with potassium (K) (correlation -0.65 for surface and -0.62 for subsoil). The similarities between the results of the two analyses can be seen in the scatter plots of the species distribution in relation to the chemical axes (Figure 4.7a and b) and as the original samples were cognate all further analyses were carried out on the surface data only.

4.5.3 Analysis of the combined effects of the physical and chemical environment

Supplementary physical data were superimposed over the species and soil chemistry CCA (Figure 4.8).

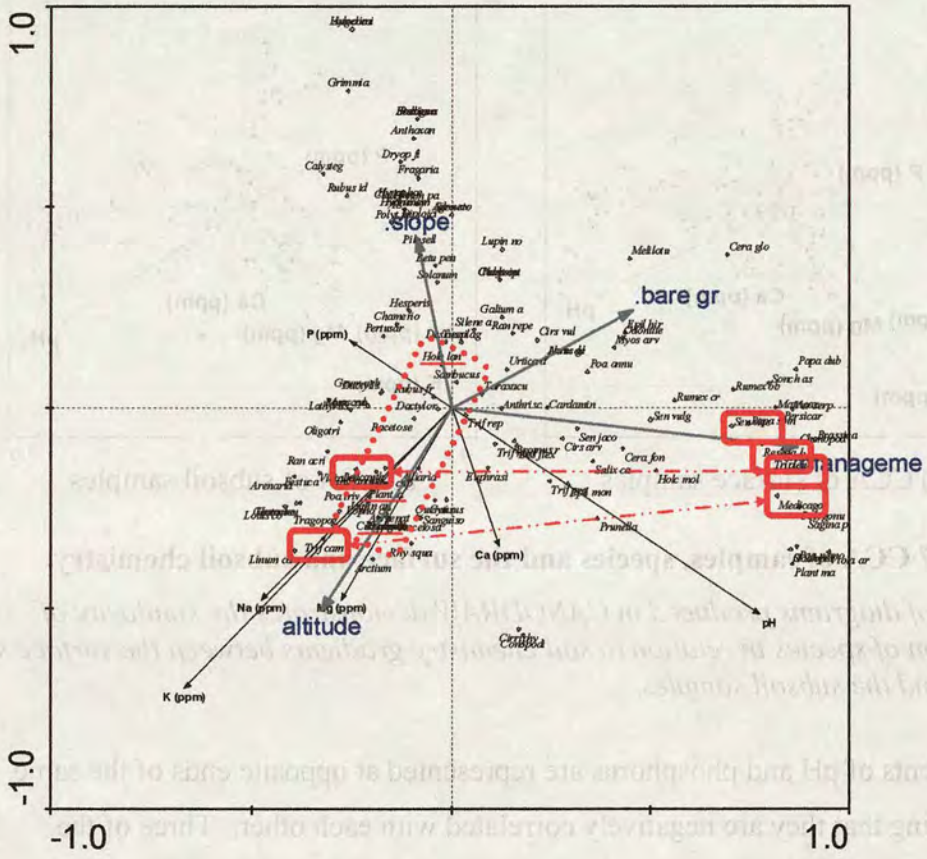


Figure 4.8 CCA of samples, species and the surface chemistry with supplementary physical data.

The species enclosed in solid rectangles are Reseda luteola *and* Senecio viscosus. *The paired species linked by arrows* Medicago lupulina *and* Trifolium campestre, *and* Leucanthemum vulgare *and* Tripleurospermum inodorum. Holcus lanatus, Centaurea nigra *and* Plantago lanceolata *are underlined within the broken rectangle.*

Both the physical and chemical environmental factors explained only a small percentage of the variance in species distribution and the cumulative percentage variance of species explained by all measured factors was 25.8%.The resulting graph showed that there was a strong negative correlation of sodium, potassium and magnesium with bare ground and positive correlation of the three nutrients with altitude. Calcium and pH showed a strong negative correlation with slope. Available phosphorus is negatively correlated with both pH and management. The relationships between the species identified in Figure 4.5 were still visible. *Reseda luteola* and *Senecio viscosus* were placed closely together in the figure. *Medicago lupulina* and *Trifolium campestre*, and *Leucanthemum vulgare* and *Tripleurospermum inodorum*, the species within the two families Fabaceae and Asteraceae, were placed further apart. The three common species were split by gradients in the analysis. *Centaurea nigra* and *Plantago lanceolata* were now showing a negative correlation with bare ground that was linked to a positive association with three chemical axes (sodium, potassium and magnesium). *Holcus lanatus* was in an indeterminate position close to the origin of all axes with a slight positive correlation to slope, that had not been obvious from the CCA by physical environment, linked to a negative correlation with calcium.

4.6 Discussion and Conclusions

The aim of this chapter was two-fold; to define the extent of variation in the physical and chemical environment between and within sites and to determine the extent that the variation was responsible for vegetation patterns and the distribution of individual species and groups of species. The degree of physical variation was measured between and within bing sites by divisions of elevation, aspect and management, and on a smaller scale within those divisions by percentage bare ground and angle of slope. The range of measurements defining divisions within each of the physical environmental factors was partly constrained by the sampling methodology used in the baseline survey and partly arbitrary. Chemical variation was also measured at the smaller scale from substrate samples collected with vegetation data and analysed for a range of nutrients. The data described the extent

of variance within each of the measured physical and chemical parameters in the substrate and confirmed the variation expected from the earlier ordination.

The ordination of recorded plant species with large-scale physical environmental factors, elevation, aspect and management, demonstrated that significant sized groups and numbers of species were only recorded in particular physical conditions. The general distribution of species throughout the bing environment was significantly determined by life history (annual or perennial) in relation to elevation, by dispersal mechanism in relation to aspect, and by pH, life history and establishment strategy (ruderal or stress tolerant) in relation to different management regimes. This was true of the baseline data, using all 211 species recorded, and of the most frequent species data, using only the 104 species that were recorded in 9 or more quadrats. When the data were analysed the assumption was made that all species had arrived naturally or with unintentional help from man, however there are occasional records of garden species on the lower slopes of some bings where there is a history of fly tipping (pers. obs.).

4.6.1 Elevation

When the baseline data were ordinated by elevation there was significant evidence that invasion by many species (109 of the 211 species recorded) is limited to one particular division within the bings, although many of these species are recorded infrequently. An additional 65 frequently recorded species are strongly associated with one of the divisions of elevation. A possible interpretation of this information is that most species (174 of 211) follow one of four patterns of distribution.

They invade:

1. from the lower elevation upwards (93 species restricted to or strongly associated with lower or lower+middle elevations)
2. from the upper elevation downwards (42 species restricted to or strongly associated with upper or upper+middle elevations)
3. from the middle elevation, both up and down (10 species restricted to or strongly associated with middle elevations only)
4. from both the upper and lower elevations toward the middle (29 species restricted to or strongly associated with upper+lower elevations)

More species were recorded at lower elevations than either middle or upper elevations and a significant number of these were restricted to the lower elevations of the sites. Statistical analysis showed that the life history of species, whether they were annual or perennial, was significant in their distribution. 43% of species associated with upper elevations were annual compared with 10-14% associated with the middle and lower elevations. This suggests that more annual species are better adapted to long range dispersal than perennials but that, since mode of dispersal was not a significant factor, these adaptations are found in species with wind, animal and unspecialised modes of propagule dispersal.

Alternatively, it is also possible that these species are not invading from the upper elevations down but are early successional species that initially covered the whole bing and are now being out-competed as perennial species invade and establish from the base. This theory is more in keeping with the traditional expectations of the processes of primary succession (Golley, 1977) but does not take into account the significant numbers of species that are associated with the middle elevations only or have a bi-modal distribution.

A further possibility is that the apparent distribution patterns of species are a function of sampling bias. Elevation was divided according to the stratified sampling strategy (Section 3.3.1) employed for the baseline survey. This resulted in top elevation vegetation data that has been recorded from a height of 12 m above the surrounding landscape and 145 m above sea level at the summit of Mid Breich, to a height of 95 m and 195 m above sea level, on the plateau of Greendykes. A sampling technique that recorded vegetation at height in metres above the surrounding landscape or above sea level would have resulted in different data sets and possibly different interpretation of ordination results[5]. If the uneven distribution of annual species is a function of sampling bias increased numbers of annuals will be

[5] Hand-held GPS equipment is now sufficiently accurate to record such measurements quickly and efficiently in the field and is often combined with inbuilt data-loggers. When the survey for this study was carried out (1999) the accuracy of most hand-held was doubtful, particularly for altitude, and the instruments frequently needed unwieldy additional equipment to log data. Traditional surveying methods were not practical because of time and manpower constraints.

associated with the upper elevation quadrat records from only a few individual sites. Examination of the ratios of annual to perennial species for individual sites showed that each site has a higher proportion of annual species recorded in the upper elevations than in the lower elevations or for the bing as a whole.

4.6.2 Aspect

More than twice as many species were recorded on the cooler (north and east facing) than the warmer (south and west facing) slopes of the bings and mode of dispersal and established strategy were the significant causal factors resulting in this distribution.

61% of species associated with cooler slopes were wind dispersed and only 16 % animal dispersed. The most likely process responsible for this distribution is the direction of the prevailing winds. Wind dispersed seeds and spores will be picked up by the wind, lifted by thermals over the summit of the bings and deposited on the leeward sides by the drop in air pressure and turbulence caused by downward slope of the bing. The north and east facing slopes (NW to SE) are sheltered from direct sunlight apart from early morning and during winter months. Species associated with these aspects will encounter predominantly cool conditions. The substrate of south and west facing slopes (SE to NW) will be warmer because of increased sunlight for most of the day but is also where species are likely to be more prone to desiccation because of the direction of the prevailing winds (as described in Section 4.2.1).

Almost half of all species recorded (103) had no association with either warm (south and west facing) or cool (north and east facing) aspects and a significantly high proportion of these, 59%, were either ruderal or stress tolerant species. Thirty-four species were unique to or strongly associated with the warmer aspects of the bings and only 10 of these (<30%) were ruderal or stress tolerant. Similarly, of the 74 species associated with cooler aspects less than 40% were ruderal or stress tolerant. Closer examination of additional growth habits of the individual species that are unique to, or strongly associated with, the two aspects might be more appropriate in determining positive causal factors in the successful colonisation of sites by species.

4.6.3 Management

Management regimes on the bings were shown to be a major causal factor in the distribution of species between and within the sites. Variation in pH, life history and established strategy were each significant to different management divisions and large numbers of species were unique to each of the divisions. Like elevation, management should ideally have been measured on a more precise scale of divisions. Data using the exact dates of disturbances and management events could be built into a chronosequence of successional events. Unfortunately, although approximate data are available for some bing sites and some periods of management (West Lothian Council, various dates), the information is patchy and does not record, for example, times of cessation of dumping within sites during their working life-time.

The varying management practices were expected to have considerable impact on the species composition of the bings and the influence of planting and seeding has already been briefly noted however the wider ramifications of management, particularly the option of non-intervention needs to be investigated more thoroughly. Of the 138 species limited by management only 37 were among the most frequently recorded. The remaining 101 species were less frequently recorded, many only in a single quadrat out of the 340. If these species are also locally rare or of ecological importance this would make the bings a major contributor to the biodiversity of West Lothian. On the old managed sites 19 of the unique species are planted or seeded, including several non-native trees and shrubs, however there is also evidence of moister areas developing with the arrival of *Cirsium palustre*, *Juncus* and *Carex* spp. and the development of heathland vegetation, *Potentilla erecta* and *Calluna vulgaris*. The new managed sites have been reshaped and planted with tree and shrub species but not seeded and as a result the unique species are mainly weedy annuals or exotics like *Papavar somniferum* (probably dispersed by the dumping of garden refuse). There are exceptions however and the only bing records of *Pleurozium schreberi* and *Racomitrium canescens* are from newly managed sites. The most important 'unique' species are probably those associated with the unmanaged sites. Seventeen species representing fourteen families were recorded only on the unmanaged sites. The group included five vascular plants and three cryptogams that are locally rare (Smith

et al., 2002). *Artemesia absinthium* is a rare introduction to West Lothian. Greendykes bing is one of only two locations in the county where it has been recorded. *Erica cinerea* is also rare, as are *Phragmites australis* and *Polemonium caeruleum. Silene vulgaris* and *Solanum dulcamara* are both found occasionally in the north of the county (Smith *et al.*, 2002). *Campylopus introflexus* is an introduced species that has only been recorded in West Lothian since 1983 but is now widespread and spreading. The list of species only recorded on unmanaged sites is not spectacular on a national scale but the local rarity of some of the species determines the importance of maintaining at least some of the bings in their current unmanaged state. The relevance of the outcome of different management practices on the bings will be discussed more completely in relation to the wider picture of biodiversity and reclamation management in Chapter Seven. This section is intended to demonstrate the extent to which management is a key factor in the distribution of species on the bings.

4.6.4 Angle of slope

Angle of slope varied considerably within the divisions of elevation, aspect and management and 104 species were limited by this environmental factor. The significant distinguishing habit of species was the distribution of annuals and perennials. A significantly high proportion of species recorded on flat ground were annuals but only a single annual was recorded on steep slopes (*Raphanus raphanistrum*) and all of the species negatively associated with flat ground (unique to or strongly associated with the gentle+steep division) were perennials. The group of 63 species unique to or strongly associated with flat+gentle slopes (0^{o} + >0-30^{o}) were not significant in number but had a significantly lower than expected proportion of wind dispersed species associated with them.

It should perhaps be taken into consideration that on many areas of the bing sites, angle of slope is an artefact of management, the result of reshaping and stabilising previously steep slopes.

4.6.5 Bare ground

There are extensive areas on the bings with limited vegetation cover and the numbers of species grouped by the divisions of bare ground are significant. However many of the species (85) were uniquely associated with lack of bare ground, including 15 species from the most frequent data set. Some of these are associated with planting and seeding and have been discussed in association with management. Other species had invaded old and new managed sites, and unmanaged sites without deliberate dispersal through management (*Lotus corniculatus* and *Potentilla erecta*).

Areas of bare ground within the larger divisions of physical environment are only rarely obviously caused by erosion in the form of landslips, water gullies or animal activity (including man and machine) and so are not usually bare due to continuous major disturbance. Species that were associated with high levels of bare ground were significantly more likely to be annual and ruderal, and none of them were associated with low pH values. A higher than expected proportion have unspecified dispersal mechanisms but are associated with agriculture (Hodgson *et al.*, 1995) and very few are animal dispersed. The species were recorded as sparsely scattered individuals and were rarely recorded in vegetation where competition for resources was high. Although the division was made at 50% bare ground several species were further limited to quadrats with 70% or more bare ground (*Reseda luteoloa* and *Senecio viscosus*). Conversely *Rhinanthus minor* and *Potentilla erecta* were only recorded in quadrats with less than 30% bare ground and *Calluna vulgaris* in quadrats with full cover. Only one of the species associated with more than 50% bare ground is considered to be stress tolerant (Hodgson *et al.*, 1995), yet lack of vegetation will extenuate any small-scale surface erosion by wind and rain, that might not be detectable to the eye, and will increase the desiccation effects of strong or continuous sunlight on south and west facing aspects as already mentioned (4.6.2). The extent that the combined effects of environmental factors are linked to the processes of species distribution will be considered in association with the section discussion of multivariate analyses (Section 4.6.7).

Cryptogams were demonstrated to be a major feature of the bing vegetation and thirty species were recorded in this study, nine of these species were represented in the most frequent data set and were shown to be limited by the measured physical environmental variables. The oil shale bing habitat is recognised as important to the diversity of bryophytes and lichens in West Lothian (Smith *et al.*, 2002) and several species are not recorded elsewhere in the county. The distribution of non-vascular species is often not described fully in general vegetation surveys because of the scale of data collection and unfortunately this study is no exception (2 m x 2 m quadrats are too large for surveying bryophyte diversity). *Hypnum cupressiforme* was recorded at all bing sites and locations within sites and has two recognised varieties: *H. cupressiforme* var. *cupressiforme* is associated with acidic environments and var. *lacunosum* is associated with basic soils and rocks (Smith, 1978). The frequency and abundance of this species alone in relation to measured variations in the substrate chemistry provides a suitable subject for further research.

4.6.6 Substrate chemistry

Species were grouped by their association with high or low pH, as discussed in relation to limited physical environmental factors in the previous sections of this chapter, and in Chapter Three the autecological similarities of the species recorded on all sites, and positions-on-site were noted. The resulting classifications suggested that analysis of the bing substrate would measure considerable variations in substrate chemistry. Chemical analysis of the substrate confirmed extremes of variation both within and between bing sites. There was a strong temptation to discard some of the exceptionally high measurements as outliers but this was resisted when samples of volcanic ash analysed for a colleague, by another laboratory but using the same techniques, showed similar variation in the same nutrients (Mr Alan Gray[6], pers. comm., 2003).

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[6] Mr A Gray is a colleague from the Ecosystem Dynamics research group within the School of GeoScience, and not to be confused with Mr A.N Gray who carried out the chemical analysis of samples.

The degree of variability in phosphorus, magnesium and calcium was much greater than expected from literature, both within and between sites. The overall expectations from literature were for a low-nutrient environment. Bradshaw and Chadwick (1980) suggested that there would be a severe deficiency of macronutrients and possibly excess salinity in the oil shale substrate. Available potassium levels were generally lower than recorded by Marrs *et al.* (1991) in a study of three contrasting substrates (chalk, clay and sand) in south-east England, and lower than expected from the characteristics recorded in spent oil-shale in Colorado (Bradshaw and Chadwick, 1980). Sodium was also measured at much lower levels than recorded from this source. The potassium and sodium levels in the West Lothian oil-shale may be washed out of the top 20 cm, or more, of substrate by 600-1000 mm yr^{-1} of rainfall in central Scotland (Meteorological Office, Edinburgh, 1990) compared with Colorado's rainfall of 250-300 mm yr^{-1} (Bradshaw and Chadwick, 1980). However, available calcium and magnesium, which are also soluble, were measured at considerably higher levels than expected. Phosphorus was likewise measured at much higher levels than expected. Nitrogen concentrations in the substrate from the two bings sampled were very low, indeed negligible, however this corresponds with measurements from spent shale in Colorado, USA (Bradshaw and Chadwick, 1980). Nitrogen is often singled out in research as the most important of the nutrients to plant growth, based mainly on anthropogenic requirements for crop growth or rapid vegetation cover. When levels of available nitrogen in the substrate are low, sufficient additional sources are usually available to plants from nitrogen fixation, organic matter in the soil and in rainfall. Organic matter is not a substantial source of nitrogen on the bing sites and is sparse throughout the substrate because of the low density of vegetation, particularly on steeper slopes. Many of the commonly recorded species have strong mycorrhyzal associations (Harley and Harley, 1987; Grime *et al.*, 1988) that enable more efficient uptake of phosphorus but only *Lupinus nootkatensis* (recorded only where planted), *Trifolium repens*, *T. pratense* (both listed in the seed mixes of management plans but also recorded elsewhere) and *T. campestre* are nitrogen fixers. Nitrogen input from rainfall must have a biologically significant effect on vegetation. In the north and west of West Lothian nitrogen is deposited at 10-15 kg ha^{-1} yr^{-1} and in the south and

east at 15-20 kg ha^{-1} yr^{-1} (Davidson, 2002). This input is small compared to a low nitrogen application in agriculture of around 80 kg ha^{-1} yr^{-1} and average nitrogen usage on wheat of 210 kg ha^{-1} yr^{-1} (Stationery Office, 1998) but is clearly sufficient to allow the successful establishment of 211 different plant species on the shale bings.

The pH levels measured between pH 5.7 and pH 8.2 in the samples taken from the bing sites. The logarithmic scale that is used to measure pH (pH 5 = 100 ppm, pH 6 = 10 ppm, pH 7 = 1 ppm, pH 8 = 0.1 ppm and pH 9 = 0.01 ppm) hides the extent of variation in the substrate. This converts approximately to 25.00 ppm - 0.08 ppm, representing weak acid (e.g. acetic acid) to weak alkali (e.g. calcium hydroxide), and highlights the confusion that can occur when using 'high' and 'low' to describe pH. The information produced by Bradshaw and Chadwick (1980) implied that pH levels would be adequate to deficient in oil shale leading to an expectation of slightly acid substrates (5-6 pH) although this appeared to contradict their textual description of oil shale.

When the variation in measured nutrients was considered in relation to individual bings and the four measured elevations, plateau, top, middle and base, each element performed differently. The newly managed bing at Clapperton had low potassium and phosphorus and a high pH but the substrate of the older managed bing, Oakbank, had 'normal' levels of potassium (Bradshaw and Chadwick, 1980), high levels of phosphorus and lower pH. This variation might be a direct result of different management regimes or related to the time since management or to heterogeneity of the original shale. Unfortunately although the management records for Oakbank are very detailed there is no available documentation for Clapperton. A similar degree of variation between sites was demonstrated at the two unmanaged bings. A wide range of values of both potassium and phosphorus were measured in the substrate from Greendykes, the largest of the bings, but the range of pH was limited. A narrower range of phosphorus and potassium was observable in the substrate of Mid Breich, the smallest of the bings, but the range of pH measurements was the greatest for all the sites. The variation in nutrients between the two unmanaged sites possibly relates to the difference in site size and volume of shale (Appendix 1). There is less

opportunity for variability in compounding physical factors, like elevation and slope, from a smaller site. A cursory glance at the boxplots of within site variations in nutrients (Figure 4.3) suggests that potassium levels increase with elevation, phosphorus levels decrease with elevation and pH levels fluctuate. This visual effect is caused mainly by the plateau data which are representative of one site only, Greendykes. If the plateau and top data are combined to represent the upper elevations from the physical environment, the boxplots suggest that the range of potassium and pH values increase with elevation, and the range of phosphorus levels fluctuate. Suggested trends in within site chemical variation may therefore be an artefact of the arbitrary division of elevation.

Having established the extent of the chemical variation in the substrate within and between the shale bings the species recorded with the sampling quadrats could have been ordinated and analysed in relation to divisions of variation in each of the measured chemical environmental factors. The decision was made not to approach the analysis this way because many of the elements interact with each other and are likely to have a combined effect on individual species. All species associations with the chemical environment were determined using multivariate analyses.

4.6.7 Multivariate analyses

Multivariate analyses corroborated much of the significant variation in species distribution determined from classification by divisions of physical environmental variables. The causal environmental factors of the relationships between some individual species also became more obvious from the multivariate analyses and there is further corroboration of connections between some species that had been noticed in the field and confirmed by TWINSPAN in Chapter Three.

The main axis produced in Detrended Correspondence Analysis of species distribution coincided with the gradient of variation in percentage bare ground. Canonical Correspondence Analyses of species distribution with the five measured physical environmental gradients consistently demonstrated percentage bare ground to be the main cause of described variance in the vegetation in the full data set and also the most frequent data set. Species limited to quadrats with more than 50% bare

ground were recorded at all elevations on the bings (upper, middle and lower) suggesting that the exposed-substrate habitat is not affiliated with other physical parameters, a theory that is corroborated by the length and direction of the bare ground axis in Figure 4.5. The clustering of the thirteen species on this axis of the CCA confirms them as a distinct group. Grime *et al.* (1988) record all of these species that were restricted to areas of highly exposed substrate on the bings as being effective colonisers of artificial and highly disturbed habitats. A CCA of the full data set demonstrated the effect of different management regimes on vegetation distribution, particularly those species that are less common, and raises questions of how bing sites should be best managed. The answers will always be dependant on the intended outcomes of management and will be discussed in Chapter Seven.

Multivariate analyses were also used to confirm the extent of variability in the chemical environment and determine the effect of individual elements on species distribution. CCA's of the distribution of species in relation to the measured nutrients in the surface and subsoil samples determined that the differences between the two sets of data were not sufficient to warrant continued separate analysis. This was not unexpected because the substrate on the bings does not conform to the accepted model of soil structure and has no recognisable horizons that might indicate a variation in chemistry with depth (Fanning and Fanning, 1989). The distribution of species in relation to the chemical variables (Figure 4.7) suggests that the main limiting chemical factors are pH and potassium (although the individual axes for sodium and magnesium are on the same alignment, potassium has the longest gradient). There are a large number of species that are negatively correlated with high concentrations of all of the measured chemical elements suggesting that variation in substrate chemistry is restricting their distribution.

The variation in available nutrients in the bing substrate was much greater than either the literature or the ordination of species attributes suggested (Chapter Three). Bradshaw and Chadwick (1980) suggest that oil shale waste is unsatisfactory for plant growth "due to alkalinity, salinity and ion imbalance", that nitrogen and phosphorus will be low and potassium rarely low. The chemical analysis of the oil shale waste on the West Lothian bings confirms that nitrogen availability is very low

and also finds that potassium levels are lower than suggested for optimum plant growth. All other measured macronutrients are sufficient, or present at potentially toxic levels. However there is no evidence from this research that the high level of some soil elements is having a detrimental effect on plant invasion on the bings or that only specialised species are establishing in the unusual substrate. The question has to be posed what is the "normal" or "optimal" growth that plant species are expected to attain under model nutrient conditions. Despite the emphasis placed on the importance of the availability of key nutrients to plant growth described in literature the percentage of described variation that could be attributed to the chemical environment was only 14% (combined described variance from all nutrient axes in CCA). The bing species can establish, survive and successfully reproduce with minimal resources or potentially toxic levels of some elements and many species are also successfully contending with extremes of heat and desiccation.

The total amount of variation in species distribution on the West Lothian shale bings that could be attributed to the physical and chemical environment, analysing all measured factors, was only 25.8%. However, multivariate analysis presumes a reasonable match between data properties. The unexplained variation in vegetation patterns in relation to environmental gradients could indicate considerable chance establishment and distribution of species or reflect the inherent plasticity within individual species when growing in a wide range of habitats. It could also be a function of the scale of measurement in the original survey. If considerable heterogeneity in either the vegetation or the physical and chemical elements of the substrate on the shale bings occurs at a scale below the 2 m x 2 m sample size the data set will not be sensitive to analysis. Smaller scale investigations of the physical and chemical environment in relation to safe sites could have revealed more significant results. These could relate particularly to individual shrubs and trees that have established in microhabitats within areas that are not generally covered by plant invasion. The influence of microtopography on vegetation has been recognised since Harper *et al.* (1961) first used the term 'safe site' to describe a microsite that is suitable for germination and establishment. Silvertown and Dickie, (1981) describe these safe sites as having sufficient water and nutrients, a soil surface that will allow

penetration by the radicle, and a topography that offers protection from desiccation. This is reiterated by Jumponnen *et al.* (1999) who describe the surface and substrate of individual microsites, their aspect, the physical and chemical conditions of the raw parent materials and the direction of the prevailing wind, as the main determinants of potential recruitment and spatial distribution of plants. These are all measurements that were made in this study or are available from climatic records and could have been collected at a smaller scale. Continued investigation relating species distribution to microsite variables could possibly explain more of the variation in vegetation patterns.

It may be necessary, however, to recognise that "some things are so complicated that it is impossible to predict what they are going to do next[7]" (Haddon, 2004). Mathematical models of natural populations of plants (and animals) exhibit an array of dynamic behaviour to the extent that "simple deterministic systems can produce chaotic dynamics" (May, 1986). This concept led to the adaptation of Chaos Theory, from physical to biological systems, by Robert May, George Oster and Jim Yorke in the early 1970's, but before attributing all of the remaining unexplained species distribution on the shale bings to anomalies of plant population dynamics and the vagaries of Chaos Theory other processes and mechanisms of distribution have to be considered.

The measured physical and chemical elements of the bing environment only explained one quarter of the variation in species distribution. The composition of species established within the bing habitats will also reflect the availability of seeds and spores, in seed rain and the soil seedbank, from species already established on the bing and those from the surrounding landscape. Other contributing factors will include the invasive potential of species, the fecundity and dispersal mechanisms of their propagules. The inherent plasticity of many plants in reaction to environmental factors is also likely to have an influence on the variation in distribution of individual species observed on the bing sites. Propagule physiology and mode of dispersal is

[7] A description of Chaos Theory attributed to a teenage boy with Asperger's Syndrome (fictional).

described by Hodgson *et al.* (1995) and is available for most common species. Existing data on abundance and frequency of species surveyed for this research could be incorporated with new data quantifying numbers of plants and seeds produced by each species to calculate seed productivity per unit area. Continued measurement and experiment could then establish the contributions of seed productivity, viability and availability to distribution patterns.

To research every one of the 211 species recorded in the baseline survey then collect and analyse the additional data is too large a project for this thesis. However several species have been identified within this research as demonstrating different aspects of vegetation distribution in relation to both physical and chemical environmental variables (Section 4.5.1, Figure 4.5 and Section 4.5.3, Figure 4.8). Nine of these have already been used to identify the extent that some unrelated species share attributes while other closely related species do not: *Senecio viscosus, Reseda luteola, Medicago lupulina, Trifolium campestre, Leucanthemum vulgare, Tripleurospermum inodorum, Centaurea nigra, Holcus lanatus* and *Plantago lanceolata.*

There is a very strong association between *Senecio viscosus* and *Reseda luteola* in all analyses by physical and chemical environment. The two species were consistently placed together on the bare ground axis in both the detrended and constrained analyses and were not separated by soil chemistry. They have very similar habitat requirements and are generally recorded on waste ground, with a basic substrate, both locally (Smith *et al.*, 2002) and nationally (Stace, 1997). They were always recorded together on patches of sparsely vegetated ground on the bings despite having different seed dispersal mechanisms (Hodgson *et al.*, 1995).

There were two pairs of closely related common species, *Tripleurospermum inodorum* and *Leucanthemum vulgare* (Asteraceae) and *Trifolium campestre* and *Medicago lupulina* (Fabaceae), that had not been recorded together in the survey and were shown to be strongly linked to different environmental axes. The analyses demonstrated that as well as having different physical requirements for bare ground the species are further separated by nutrient availability. Ellenberg indicator values

(Hill *et al.*, 1999) suggest that *T. inodorum* has a higher nitrogen requirement than *L. vulgare* and that *T. campestre* does not require such fertile soil as *M. lupulina* but again there is a lack of comparable data recorded in the literature. The patterns may be linked to dispersal mechanisms and survival ability.

Three very common species, both on the bings and in the surrounding landscape, *Holcus lanatus*, *Centaurea nigra* and *Plantago lanceolata* always appear clustered together, close to the origins of the physical environmental axes in the multivariate analyses. This indicates that the species have a very broad range of habitat requirements, and all sources agree that they are generalists (Smith *et al.*, 2002; Stace, 1997; Grime *et al.*, 1988). *C. nigra* and *P. lanceolata* were separated from *H. lanatus* along the sodium (Na) axis in the CCA of soil chemistry. The apparent variation in sodium requirement is intriguing and could be important to these species as they become forced into man-made and post-industrial habitats through the loss of more natural habitats. There is no provision in this study for continued investigation into individual species requirements for soil nutrients or adaptations within species to the excessive availability of some common elements in the oil-shale substrate. There is a lack of available information in this area that should be addressed by experiment and field investigation, particularly for species and genera outside agriculture and horticulture.

The extent that variation in the distribution of each of the nine species is limited by elements of the physical and chemical environment can be calculated from existing data and analyses. The next chapter will describe the collection of the additional data required to establish the extent that species numbers, seed availability and viability explain the so far unexplained variation in distribution of these nine species.

4.7 Summary

The initial aim of this chapter was to define the extent of variation in the physical and chemical environment of the substrate of oil-shale bing sites suggested from the ordination of vegetation described in Chapter Three. From the literature there was conflicting information on the physical and chemical environment that should be

expected on the shale bings making the generation of hypotheses difficult. A range of ordination and analysis techniques established that the scale of variability within each of the measured features was considerable. The environmental data were then ordinated with species data so that vegetation patterns, and the distribution of individual species and groups of species, could be defined within the context of measured physical and chemical variation in the substrate. From this it was possible to demonstrate that vegetation patterns are associated with environmental gradients and that species composition reflects gradients in both the physical and chemical environment. The absence of soil, in the biological sense, does not seem to be a major limiting factor to the colonisation process although it may restrict the invasion and establishment of individual species that are not suited to the substrate. Several very common species from the areas surrounding the bings were not recorded in quadrats or observed in the habitat, notably oil-seed rape (an agricultural variety of *Brassica napus*) and *Papaver rhoeas* (common poppy), both plants that have self-seeded on a range of other disturbed sites throughout the county. The causal factors for species not being present are difficult to ascertain and it is possible that several species are actually established on the bing sites but were not recorded.

The groups of species and individuals that were identified as limited by one or more measures of physical environment were found to share similar characteristics and to be further constrained by association with chemical environmental factors. The ordination of physical features demonstrated that significant groups of species were associated with the large-scale topography of the bings and that the groups could be differentiated by the shared ecological traits of individual species.

- Vegetation with a significantly higher proportion of wind dispersed species was recorded at the plateau and top positions of sites.
- Significant groups of species were associated with high and low percentages of bare ground.
- Other species were associated with different management practices, including a significant group of species that were only recorded at bing sites where there had been no management. The relevance of species limited by different management regimes will be discussed in Chapter Seven.

Within the large-scale vegetation composition there were also groups of species that were limited by angle of slope and, to lesser extent, by aspect. Distribution patterns

within bing sites were also shown to be constrained by gradients in substrate nutrients, particularly pH and potassium.

The observed vegetation patterns were determined to some degree by all of the processes measured and some processes were observed to have greater effect than others. However the cumulative percentage variance of species explained by all of the physical and chemical factors measured is only 25.8%. Further, more detailed examination of the distribution and growth patterns of nine of named species, identified as representative of particular bing habitats, may explain some additional variance and recognise further mechanisms and processes of colonisation and vegetation dynamics in the bing ecosystems. These will be investigated in Chapter Five.

CHAPTER FIVE

"It is not the strongest of species that survive, nor the most intelligent, but the ones most responsive to change."

Charles Darwin (1861) *On the Origin of Species by Means of Natural Selection*, 3rd ed. John Murray, London

5 Variation in Morphology, Productivity and Dispersal in Selected Species

In Chapter Four only 25% of the variance in species distribution was explained by the physical and chemical factors measured on the shale bings. Significant groups of species were revealed to be associated with gradients in the physical and chemical environment and these species were shown to be associated with distinct mechanisms of dispersal or growth habit. The aims of this part of the investigation were to explain at least some of the remaining variance by studying the patterns of distribution and growth in a few selected species in relation to seed dynamics: measured as availability, dispersability and fecundity, and morphological plasticity represented by plant height. The questions being addressed are:

How great a determining factor in the establishment of vegetation is the availability of seeds and spores in seed rain and the seedbank?

Is phenotypic plasticity a major contributor to vegetation dynamics at individual species level?

Is any variation in seed production within a species correlated with either height or number of flower-heads?

Will local site conditions have a direct effect on the size of individual plants within a species, measured as height above ground, and hence on the number of flower-heads and seeds produced?

In previous chapters species associations, general vegetation patterns and correlations have been identified using all species, or the most frequent species, recorded on all sites. As suggested in Chapter Four it would be impractical to gather the additional information required from all 211 species recorded on the shale bings,

or even to use the 100 most frequent species. In this chapter within species variation in morphology and the mechanisms of seed dynamics are investigated using the nine species that were identified in the previous chapter as being representative of some feature of vegetation distribution in relation to the physical and chemical environmental variables measured in the bing habitat.

5.1 Plasticity and seed ecology

Phenotypic variation can often be more clearly perceptible than genotypic variation within the same species. Plasticity enables individuals of a species to survive in non-optimal conditions, making it possible for the species to survive over several generations, until new, better-suited, genotypes are produced. The inherent plasticity in most plant species enables individuals, developing from the seedlings of a single plant, to vary considerably in height, number of flowering heads produced and number of seeds per flowering head.

The availability of seeds and other propagules in a primary succession is a major contributing factor to the patterns of colonisation. The input of propagules is not limited to those produced by populations of species in the immediate locality. Initial recruitment is often from long range dispersal, particularly when the new substrate covers a large area or is very high compared to the surrounding landscape (Cronk and Fuller 1995), as is the case on shale bings. As establishment of species increases there are additional sources of invasion within the site, from the seedbank, and from seed rain. Legg *et al.* (1992) related the numbers of seeds produced by *Calluna vulgaris* to those recorded in seed rain, the seedbank and to the final outcome of the vegetation. Seed rain patterns in New Zealand were linked to vegetation patterns in successional seres by Dungan *et al.* (2001). Similar correlations are expected between the patterns of seed rain falling on the bings and the resulting vegetation.

The number of flowering heads and seeds per flowering head that are produced by individuals from the selected species is expected to be linked with variation in the height of adult individuals within the species recorded on the bing sites. Zammit and Zedler (1993) established that in the obligate-seeding shrub *Ceanothus greggii* height

was the major determinant of seed production and the total display area of flowers was shown to be relative to overall plant size in a study by Fabbro and Korner (2004). The viability of any seeds produced is expected to be equally important to the establishment of species in the vegetation succession. It would therefore seem appropriate to concentrate on these areas for further experiment and analysis.

5.2 Nine species

In many studies detailed examination is made of one dominant species (e.g. *Calluna vulgaris*, Legg *et al.*, 1992) or species representing a particular ecological type (e.g. nitrogen fixing plants, Burden, 1980a: 1980b). The small-scale heterogeneity of vegetation recorded on the bing sites (up to 29 species in a single 2 m x 2 m quadrat) made selection of species on the basis of dominance alone very difficult. Recognised ecological types and functional groups of species (as described in Burden and Harper, 1980) were not associating as expected in the vegetation of the bings: partly because of the influence of planting and seeding and partly because of the early stages of development of vegetation types, as was demonstrated by the apparently wide range of National Vegetation Classification types identified in Chapter Three (3.1.3). Analysis of the baseline survey data from eight oil-shale bings did however identify groups of species that were representative of three local ecological habits:

1. Species belonging to the same family and sharing many ecological traits, that were rarely, if ever, recorded together on any of the bing sites despite being locally abundant (in West Lothian).
2. Species that were commonly recorded on the bings but that were rarely found in the surrounding environment.
3. Species that were abundant and common to both the bing sites and the surrounding habitats.

A further group representing species that were commonly recorded in the surrounding environment but that were rarely or never recorded on the bings could also have been investigated. Such a study was beyond the resources of this exercise and would have required the collection and analysis of large amounts of new data from a variety of sites in the surrounding countryside.

Nine 'weed' species (Table 5.1) that demonstrated these three ecological types were selected for further study and measurement as described in Chapter Four (Section 4.6.7). In this way the processes and mechanisms of vegetation succession could be described in terms of individuals within individual species that are representative of each of the described types.

Table 5.1 The Nine Species

The binomial, authority, common name(s) and family for each of the nine species used in the trials and data analyses in this chapter

Species	Authority	Common name	Family
Medicago lupulina	L.	black medick	Fabaceae
Trifolium campestre	Schreb.	hop trefoil	Fabaceae
Leucanthemum vulgare	Lam.	ox-eye daisy, moon daisy	Asteraceae
Tripleurospermum inodoratum	(L.) Sch. Bip.	scentless mayweed	Asteraceae
Reseda luteola	L.	dyer's rocket, weld	Resedaceae
Senecio viscosus	L.	sticky groundsel	Asteraceae
Holcus lanatus	L.	Yorkshire fog	Poaceae
Centaurea nigra	L.	common knapweed, hardheads	Asteraceae
Plantago lanceolata	L.	ribwort plantain	Plantaginaceae

Two pairs of species were selected to represent the first ecological type. The two species *Medicago lupulina* and *Trifolium campestre* represent one plant family, Fabaceae. The two species are similar in appearance (Figure 5.1) and share many ecological traits. Although they were recorded together on only one bing site, Addiewell south, the two species were distributed differently (*T. campestre* at the top and middle and *M. lupulina* in the excavated area). The two species were not recorded together on any of the other bings in the baseline survey, despite *T. campestre* appearing in 46 quadrats and *M. lupulina* in 40 (out of 340 quadrats). Species distribution maps of West Lothian demonstrate that variation of distribution between the two species extends throughout the county (Figure 5.1).

Leucanthemum vulgare and *Tripleurospermum inodorum*, Asteraceae family, are a second pair of similar looking species that were frequently recorded (Figure 5.2). *L. vulgare* was recorded in 124 quadrats on six sites, *T. inodorum* 38 quadrats on four sites. The two species were found on the same sites, and positions within sites,

but were only recorded growing together within nine quadrats at Clapperton on ground recently disturbed by planting.

Reseda luteola and *Senecio viscosus* were selected to represent the second ecological type. These species are not found locally in other habitats and were only recorded in areas of the bing sites with little or no competition from other vegetation (Figure 5.3). They were frequently recorded with *Myosotis arvensis* in quadrats with a large percentage of bare substrate, usually at high altitudes and on steeper slopes and have traits that are traditionally associated with early colonisers.

The final ecological type is represented by three species that are common perennial 'weeds' and are found over a wide range of habitats. *Holcus lanatus*, *Centaurea nigra* and *Plantago lanceolata*, were selected because they were constant to all bing sites, altitudes and aspects and were also commonly found in the surrounding habitats (Figure 5.4).

The nine species are all native, locally common weeds (Smith *et al.*, 2002) and have been recorded consistently in numerous studies of colonisation over the last 100 years indicating that as well as being common weed species they are an important component of early successional vegetation. Brenchley & Adam (1915) recorded their appearance and fluctuations in abundance over more than 20 years in a study of two sites left fallow after cultivation. They were also recorded in vegetation surveys of a range of post-industrial sites including stone quarries (Hepburn, 1955; Davis, 1982) and disused pits (Hall, 1957). The germination characteristics of the nine species have been described in a major study of the Sheffield flora by Grime *et al.* (1981).

The nine species are all indicative of low shade, moist free-draining soils, neutral-basic soils and sites of intermediate fertility (Hill *et al.*, 1999) and with the exception of *Centaurea nigra*, rely on a persistent seedbank as a major regeneration strategy (Hodgson *et al.*, 1995). The autoecological traits, characteristics of reproduction and seed ecology for each species, as presented in these publications (Table 5.2), can be used for comparison with the measured data from this study.

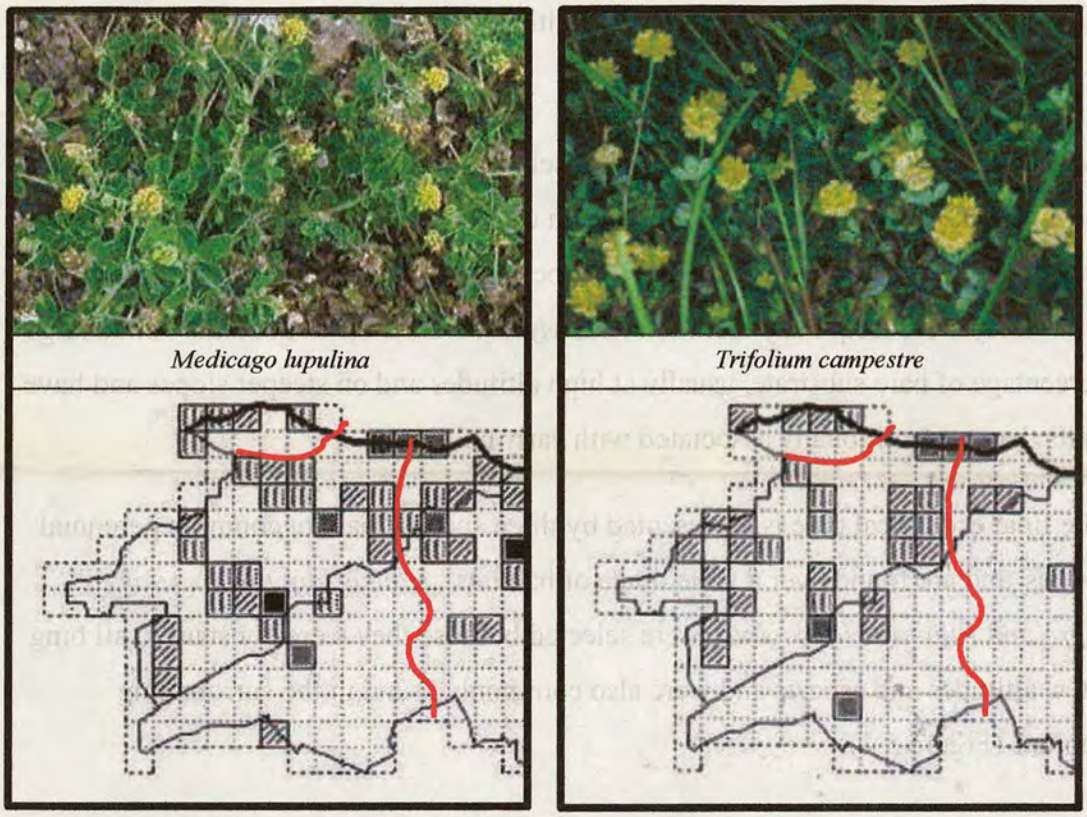

Figure 5.1 *Medicago lupulina* and *Trifolium campestre* (Fabaceae)

Medicago lupulina *and* Trifolium campestre, *the two Fabaceae species (photographs from Bioimages, undated), demonstrating their similarity in appearance and growth form are displayed above distribution maps of both species adapted from Plant Life of Edinburgh and the Lothians (Smith* et al., *2002). Within West Lothian (the political county boundary is marked in bold where it does not follow the vice county boundaries)* M. lupina *and* T. campestre *were each recorded in 26 tetrads*[1] *and were recorded together in only 15 of these. There are a total of 134 tetrads within the political boundary of West Lothian (as described in Chapter Two), 54 of these are in (or partly in) Vice County 83 (Edinburghshire / Mid Lothian) and 80 are in Vice County 84 (Linlithgowshire / West Lothian).*

[1] "Each tetrad is made up of four 1 km x 1 km squares. One square in each tetrad was then chosen at random as the square to be surveyed." Plant Life of Edinburgh and the Lothians, page 184 (Smith *et al.*, 2002).

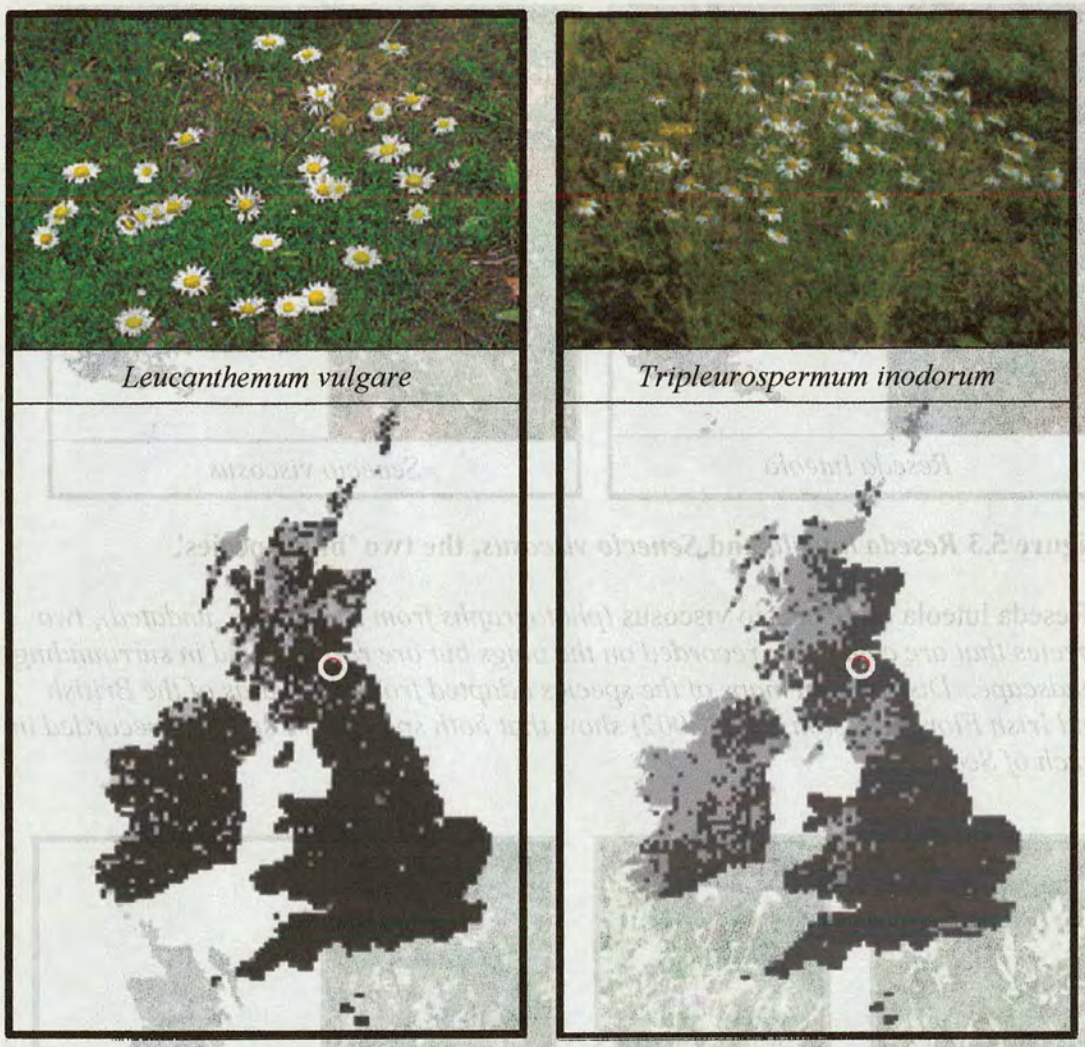

Figure 5.2 *Leucanthemum vulgare* and *Tripleurospermum inodorum* (Asteraceae)

Leucanthemum vulgare *and* Tripleurospermum inodorum *(photographs from Bioimages, undated), the two Asteraceae species, demonstrating their similarity in appearance, but different growth form are displayed with distribution maps of both species adapted from New Atlas of the British and Irish Flora (Preston* et al., *2002) showing the extensive distribution of these two species. White circles outline West Lothian and highlight that* T. inodorum *is less widely recorded in the county than* L. vulgare.

Figure 5.3 *Reseda luteola* and *Senecio viscosus*, the two 'bing species'

Reseda luteola *and* Senecio viscosus *(photographs from Bioimages, undated), two species that are commonly recorded on the bings but are rarely found in surrounding landscape. Distribution maps of the species adapted from New Atlas of the British and Irish Flora (Preston* et al., *2002) show that both species are sparsely recorded in much of Scotland.*

Figure 5.4 *Holcus lanatus*, *Centaurea nigra* and *Plantago lanceolata*, the three 'common species'

Holcus lanatus, Centaurea nigra *and* Plantago lancolata *(photographs from Bioimages, undated), three species that are commonly recorded on the bings and are very common in the surrounding landscape. The distribution map of* P. lanceolata *adapted from New Atlas of the British and Irish Flora (Preston* et al., *2002) shows the widespread distribution of this species throughout Britain. The distributions of* C. nigra *and* H. lanatus *are equally widespread.*

Table 5.2 The nine species their main autoecological traits, reproduction and seed characteristics

The nine plant species selected for detailed investigation are grouped as described in Section 5.2 above. Nomenclature follows Stace (1997) and the species are listed with information on life history, establishment strategy, regenerative status, seedbank, most common terminal habitat, soil pH, agency of dispersal and seed (dispersule) weight (Hodgson et al., *1995) and their allocated Ellenberg indicator values for light (L), moisture (F), reaction (R) and nitrogen (N) (Hill* et al., *1999).*

Habitat key: OUTCRP = rock outcrop; QRYl = limestone quarry spoil; ARABLE =arable; COAL = coal-mine spoil; CINDER = cinder tips; PASTe = enclosed pasture; WASTEl = wasteland on limestone strata; MEADOW = meadows.

Soil pH key: The numeral indicates the modal pH class for the species followed by a letter indicating the number of pH classes in which the frequency of the species exceeds 50% of that in its modal class. Thus 5a indicates that the species is most frequent within the range 5-5.9 and has a range of only 1pH unit. In contrast 4d indicates a mode within the interval pH 4-4.9 and a range of 4 pH units.

Agency of dispersal key: ANIMa = animal dispersed, dispersule with awn; ANIMm = animal dispersed, dispersule adhesive from mucilage; UNSP = unspecialised; UNSPag = unspecialised but dispersed as a result of agricultural practices; WINDc = wind dispersed, seeds small and shed from a capsule held above the surrounding vegetation; WINDp = wind dispersed, dispersule plumed or wrapped in hairs.

Seed weight key: 1 ≤ 0.20mg; 2 = 0.21-0.50mg; 3 = 0.51-1.00mg; 4 = 1.01-2.00mg; 5 = 2.01-10.00mg; 6 > 10.00mg.

Life history key: Aws = annual; As = summer annual; Aw = winter annual; P = perennial; B = biennial.

Established strategy key: primary strategies are C = competitor; S = stress-tolerant; R = ruderal; secondary strategies are CR = competitive ruderal; SC = stress-tolerant competitor; SR = stress-tolerant ruderal; CSR = CSR strategist; there are twelve further strategy intermediates between these seven (e.g. CR/CSR) making a total of nineteen types.

Regenerative status key: Bs = a persistent bank of buried seeds or spores; S = seasonal regeneration by seed; V = lateral vegetative spread; W = regeneration involving numerous widely dispersed seeds or spores.

Seedbank key: 1=transient: seed rarely persisting for more than 1 year; 2 = short-term persistent: seed persisting for more than one year but usually less than five; 3 = long-term persistent: seeds persisting for at least five years and often much longer

Indicator values key: L (light) ranging from 1 (plant in deep shade - none in UK) to 9 (plant in full light); F (moisture) ranging from 1 (indicator of extreme dryness) to 12 (submerged plant); R (reaction) measured as "the gradient of soil acidity and lime content"[2] ranging from 1 (indicator of extreme acidity) to 9 (indicator of base reaction); N (nitrogen) is a general indicator of soil fertility ranging from 1 (extremely infertile) to 9 (extremely rich).

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[2] The reaction scale is not synonymous with the divisions of the full pH scale (0-14) but is a scale indicative of the range of acidity and alkalinity found in European soils (Ellenberg, 1988).

Species	Habitat	Soil pH	Agency of dispersal	Seed weight	Life history	Established strategy	Regenerative status	Seed bank	Indicator values			
									L	F	R	N
Medicago lupulina	OUTCROP	7a	UNSP	5	A/P	R/SR	Bs	3	7	4	8	4
Trifolium campestre	OUTCROP	6c	ANIMa	2	Aw	SR	S,Bs	3	8	4	6	4
Leucanthemum vulgare	QRYl	7a	UNSPag	2	P	C/CSR	V,S,Bs	3	8	4	7	4
Tripleurospermum inodorum	ARABLE	6c	UNSPag	2	Aws	R	S,Bs	3	8	5	6	6
Reseda luteola	COAL	6b	WINDc	2	B/P	R/CSR	Bs	3	7	4	8	6
Senecio viscosus	CINDER	7c	WINDp	3	As	R	W,Bs	3	8	5	7	6
Holcus lanatus	PASTe	5c	UNSP	2	P	CSR	V,S,Bs	3	7	6	6	5
Centaurea nigra	WASTEl	7c	UNSP	5	P	CSR	V,S	2	7	5	6	5
Plantago lanceolata	MEADOW	7c	ANIMm	4	P	CSR	V,Bs	3	7	5	6	4

The baseline survey established that all nine of the selected group were within the top fifty species (out of 211) by both frequency and accumulated percentage cover on the bing sites. Four of the species selected were among the twenty most frequently recorded and among the twenty species with the highest accumulated percentage cover (*H. lanatus*, *L. vulgare*, *P. lanceolata*, and *C. nigra*). *S. viscosus* was also in the twenty most frequently recorded species and *M. lupulina* in the twenty species with highest accumulated percentage cover. The species were all recorded on the three main positions-on-site, top, middle and base, although *T. inodorum* and *M. lupulina* were not recorded on the plateaux and *C. nigra*, *R. luteola* and *L. vulgare* were not recorded on the excavated sites. The nine species grew successfully at all aspects (north, south, east, west, northeast, southeast, southwest, northwest) and on slopes up to 60 degrees from horizontal except *T. inodorum* which was only recorded on slopes up to 40 degrees. *S. viscosus* and *R. luteola* were not recorded in quadrats with more than 40% ground cover although the other seven species were recorded in quadrats containing all levels of ground cover. This suggested that variation in physical environmental gradients could be ruled out as a major determining factor in the distribution of the species with the possible exceptions of *T. inodorum* (angle of slope) and *S. viscosus* and *R. luteola* (competition from other species). These three species were also absent from quadrats recorded on the old managed areas of the bings as defined in Chapter Four (Section 4.2.1).

5.3 Measurements and trials

The extent of morphological variation within and between species was measured and counted in the nine selected species: height (representing plasticity), number of flowering heads produced and number of seeds produced per flowering head. A series of field experiments and glasshouse trials were established to measure the species components of the substrate seedbank and seed rain on the bing sites, and the germination potential of seeds collected in the field. The resulting data were analysed to establish whether height varied within and between species as a response to individual environmental factors and to determine any relationships between variability in height and the mechanisms and processes of seed production, dispersal

and germinability within each species. The resulting information demonstrated to what extent the variation in seed dynamics and morphological variability within these species is the cause of variance in the distribution of vegetation.

5.3.1 Plant height and seed production

The number of individual plants growing in each 16 m^2 quadrat block (as described in Chapter Four) was recorded for each of the nine species. The heights of ten randomly selected plants of each species were measured (from the surface of the substrate to the highest point of the plant) and the total number of flowering heads (immature and mature) per plant were counted and recorded. Ten representative, mature flowering heads were selected from each plant and the number of seeds were counted and recorded. If ten individuals of any species were not represented in the quadrat and plants were growing within a further 1 m of the block in any direction then these were measured but not included in the plant count for the quadrat. If there were no flowering heads on the selected plant or no seeds in the selected flowering head these were recorded as zero values. Forty quadrat blocks were surveyed in this way, 12 at Oakbank, 12 at Clapperton and 16 at Greendykes. Counting was abandoned at Mid Breich due to overlapping ranges at the top and middle positions-on-site on this very small bing. All further trials and measurements relate to only three sites: Greendykes, Oakbank and Clapperton.

5.3.2 Seed and seedling identification

Samples of seed were collected from as many species as possible during the field seasons, while still attached to the plant, and were used to produce a seed 'herbarium' for use in the identification of samples from seed rain and the seedbank. An herbarium of seedling stages was compiled for grasses, and other vascular species that were expected to have less easily identifiable leaf morphologies, by germinating known seeds and harvesting samples at regular intervals.

5.3.3 Glasshouse germination trials

Seeds for germination trials were collected in late autumn 1999 from plants of each of the nine species that were growing in and around the fixed quadrat blocks. Two hundred and forty seeds from each species were sown in 12 individual plant pots

(10 cm diameter) filled with vermiculite growing medium, twenty seeds to a pot. Thirty six pots were prepared without seeds as controls. Nine pots, one sown with seed from each of the species, and three control pots were randomly positioned on each of 12 trays (a total of 144 pots). The trays and their contents were then randomly positioned in the heated mist unit of a glasshouse on 10th October 1999.

The trays were first inspected after one week, then on Monday, Wednesday and Friday of each week thereafter. Germinated seeds were counted and removed with as little disturbance as possible on each occasion. After 8 weeks, when there had been no new germination recorded for 2 weeks, the trays were removed to cold frames and monitored weekly. There was then no germination for several months until a series of frosts at the end of April 2000 after which additional germination was recorded. Weekly monitoring was terminated in August 2000 after three months with no further germination from any of the species.

5.3.4 Soil seedbank trial

A seedbank trial was set up to examine the availability of propagules from this source. Substrate samples for seedbank analysis were collected from the same fixed quadrat blocks as were used for chemical analysis (Chapter Four, section 4.2.2) plant measurements (5.3.1) and collecting seeds (5.3.2). The 300 g that was retained from each of the bulked and concentrated substrate samples (Chapter Four, Section 4.2) was spread in a 25 mm layer (Fenner, 1985) over sharp sand in a 150 mm x 200 mm seed tray. The resulting 100 seed trays, containing 50 surface soil samples and 50 unweathered substrate samples, plus an additional ten control trays containing only sand were set out randomly in the mist unit of a heated glasshouse. The trays were monitored for 3 months (Thomson *et al.*, 1997) and seedlings were identified by comparison with a collection of seedlings from known parent plants (5.3.2) and counted as soon as possible after they emerged, then removed. Any unrecognised seedlings were identified using Williams & Morrison (1987) and Hanf (1974). All individuals, of all species germinating, were recorded. At the end of the 3-month period the substrate in each tray was hand sorted to find any propagules that had not germinated.

5.3.5 Seed traps

The open nature of the shale bings, both to the elements and the public, meant that standard (commercial) equipment for seed trapping could not be used. Seed traps were designed to be as inconspicuous as possible. The traps were constructed from empty 2 litre soft drinks bottles, wire mesh (5 mm x 5 mm to avoid trapping small mammals) and either sections of 20 denier tights or filter paper (Figure 5.5a). Prototypes of both versions were tested in various positions in a garden to ensure that they functioned effectively. The two versions of the trap worked equally well and I elected to use the filter paper version because it was slightly easier to construct.

The seed traps were set at ground level (Figure 5.5b), one in each of the forty quadrat blocks used for substrate analysis. The traps were placed in a randomly selected hole, one of ten, left by the removal of substrate for the seedbank trial.

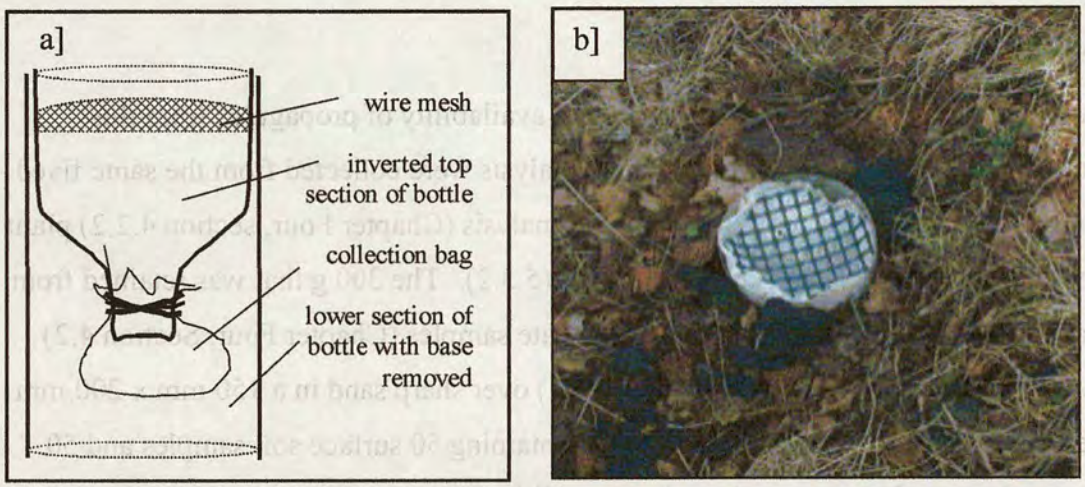


Figure 5.5 Seed traps

a] Seed trap with collection bag made from sections of tights fixed with an elastic band and b] photograph of a seed trap with filter paper insert in situ *at Oakbank bing.*

Unfortunately there were no results from the seed traps on any of the sites. Both variations of the seed trap were set out on two or more occasions but when revisited for seed collection were found to have been scattered and destroyed by Corvids (probably rooks or jackdaws) at all sites and this attempt to measure seed rain had to be abandoned.

5.3.6 Analysis of data

The correlation analysis tool in Microsoft Excel was used to measure any relationship between the data sets of morphological measurements for each of the nine species; plant height, population density, number of flower-heads and number of seeds. The coefficient of variance (CV) was calculated to compare within species variation between the morphologically different species (CV = 100 x SD / mean).

Variation between the seedbank data for the nine species linked to either the surface samples or the unweathered samples was tested by calculating χ^2 , supported by G-test and Fisher's Exact test (Chapter Four, Section 4.2.1 and Legg, 2004), for statistical significance. This method of analysis would also show if there were any significant differences between the germination patterns of the nine species and all other species germinating from the seedbank.

Canonical Correspondence Analysis (CCA), using the CANOCO 4.5 program (ter Braak and Šmilauer, 2002) determined whether the variation in morphological measurements of the nine species could be explained by the physical and chemical environmental data recorded from the sampled 50 quadrat blocks (Chapter Four, Section 4.2). The species abundance data matrix that was part of the multivariate analysis described in Chapter Four (Section 4.2.3) was replaced with either a plant height matrix, number of flower-heads matrix or number of seeds produced matrix constructed from the morphological measurements collected in the same quadrat blocks (Section 5.3.1). A species presence absence matrix was added to the analyses as a covariable with the morphological data after an exploratory analysis (CCA) highlighted how strongly this factor was linked with environmental variables. A $\log_n$ transformation was performed on the seed matrix because of the extremely large inter- and intra specific variation in numbers of seeds recorded.

5.4 Results of field measurements

Individual representatives of the nine species were measured in the field to gauge variability in height (from substrate to highest part of plant). The numbers of each species were counted and recorded as were the numbers of flowering heads and seeds

produced per head (Section 5.3). Population density and seed production were calculated from the resulting data (Table 5.3).

5.4.1 Plant height

The numbers of plants that were measured for height varied between species because not all nine species grew in every quadrat block. Sixty individuals of *Tripleurospermum inodorum*, the least abundant of the nine species, were measured in 6 quadrat blocks and 210 individuals of *Holcus lanatus* were measured in 21 quadrat blocks. All of the plants measured were producing flowers and/or seeds and were therefore assumed not to be juveniles. There was considerable variation in the measured heights of individual plants within each of the nine species (Figure 5.6 and Table 5.3).

The two Fabaceae species, *Medicago lupulina* and *Trifolium campestre*, had similar median height, and were measured over a similar range of heights (Figure 5.6). The coefficient of variance (CV) of both species was high (approximately 80%) but the maximum measured height for *M. lupulina* in this study was only half of the published (usual) maximum (Table 5.3).

The two Asteraceae species, *Leucanthemum vulgare* and *Tripleurospermum inodorum* also had similar median height although *L. vulgare* was measured over a much greater range of heights (Figure 5.6). All of the *T. inodorum* plants measured were within the published range of usual measurements for the species and had the lowest CV of all nine species (39%) but *L. vulgare* was recorded at heights significantly different from expected, both higher and lower (Table 5.3).

Reseda luteola and *Senecio viscosus* were representative of the same bing habitat, although their morphologies are completely different. As expected *R. luteola* was by far the taller of the two species and demonstrated a greater coefficient of variance than *S. viscosus* (Table 5.3). The measured heights of *R. luteola* were significantly different from the published range, both higher and lower, but the measured heights of *S. viscosus* were significantly lower, with a maximum height of less than the mid point of the published range.

Table 5.3 Field results and calculations for the nine species

Height: The measured range of height for each species is compared with the published, usual range of height in the British Isles, taken from Stace (1997). The coefficient of variation (CV = 100 x standard deviation / mean) contrasts the degree of variance in measured height between the nine species

Density: Mean density for each of the nine species was calculated from the sum of the number of individuals counted in each quadrat block divided by the combined area of the 40 blocks (640 m^2)

Seed production: The minimum and maximum number of flower-heads per plant counted in the field and of seeds per flower-head is presented. The actual minimum and maximum number of seeds produced on any one plant was calculated for each of the nine species. The potential maximum seed production was calculated by multiplying the highest count of flower-heads recorded on any plant in the species by the highest count of seeds recorded on any flower-head in the species.

Species / Measurements	*Medicago lupulina*	*Trifolium campestre*	*Leucanthemum vulgare*	*Tripleurospermum inodorum*	*Reseda luteola*	*Senecio viscosus*	*Holcus lanatus*	*Centaurea nigra*	*Plantago lanceolata*
Range of measured height (mm)	30-400	10-350	20-980	140-430	110-1750	20-230	70-830	220-1220	50-890
Coefficient of variation (%)	79.5	80.4	83.1	38.9	87.6	68.7	69.4	50.4	74.7
Range of published height (mm)	50-800	20-300	200-750	100-600	500-1500	100-600	200-1000	150-1000	100-500
Density (m^{-2})	0.12	0.15	4.49	0.13	0.18	0.46	2.25	2.66	0.96
Flower-heads per plant									
minimum	18	1	1	1	1	1	1	1	1
maximum	723	64	51	14	19	37	71	411	21
Seeds per flower-head									
minimum	9	18	72	29	1187	29	33	27	3
maximum	33	44	340	93	1899	64	270	31	103
Seed production per plant (actual)									
minimum	162	18	72	29	1329	29	33	27	3
maximum	13737	500	8313	930	32718	882	4161	11508	1442
Potential maximum	*23859*	*2816*	*17340*	*1302*	*36081*	*2368*	*19170*	*12744*	*2163*

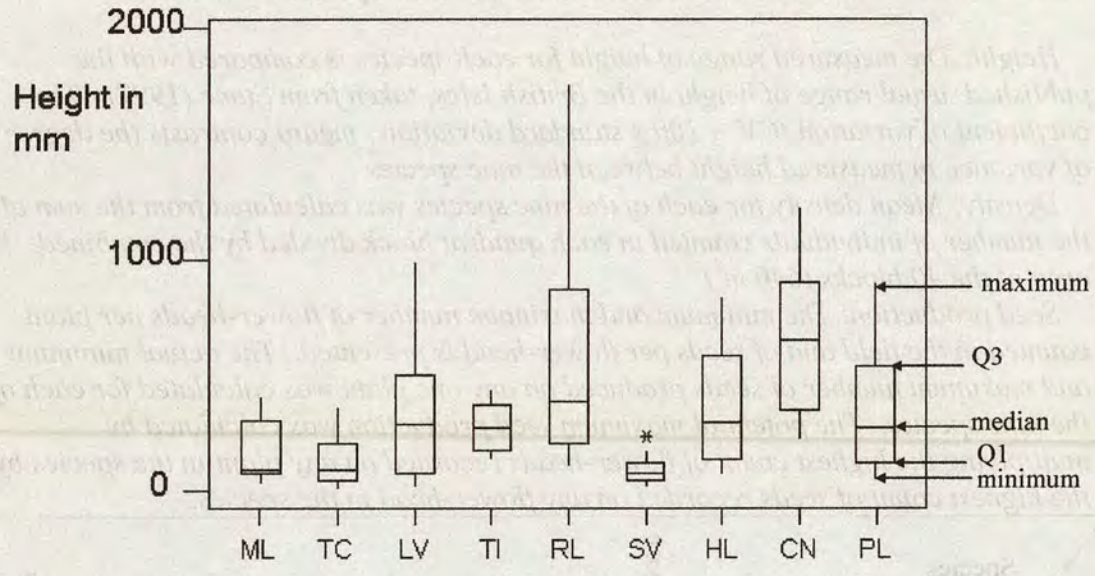


Figure 5.6 Height variation in the nine species

Boxplots showing the median, range and interquartile range (middle 50% of data, Q1-Q3) of height measured in each of the nine species. The asterisk (*) identifies an outlier in the data; a single measurement with a value lying between 1.5 and 3 times away from the middle 50% of the data (Minitab, Inc., 2000)
ML = Medicago lupulina, *TC* = Trifolium campestre, *LV* = Leucanthemum vulgare, *TI* = Tripleurospermum inodorum, *RL* = Reseda luteola, *SV* = Senecio viscosus, *HL* = Holcus lanatus, *CN* = Centaurea nigra, *PL* = Plantago lanceolata.

The three common species, *Holcus lanatus*, *Centaurea nigra* and *Plantago lanceolata*, displayed a similar inter-quartile range of height, although *C. nigra* measured taller than the other two species (Figure 5.6). The CV for *C. nigra* was 50%; considerably lower than the other species, except *T. inodorum*. When compared with the published range of usual heights, *H. lanatus* measured lower than or within the lower ranges, *C. nigra* measured higher or within the higher ranges, and although the interquartile range of *P. lanceolata* measurements were within the published range, there were both higher and lower measured heights (Table 5.3).

5.4.2 Density

There was considerable variation in the population densities of each of the nine species (Table 5.3) from one individual every 7 - 8 square metres, *Trifolium campestre, Medicago lupulina* (both Fabaceae) and *Tripleurospermum inodorum*

(Asteraceae), to one individual every 0.22 square metres, *Leucanthemum vulgare* (Asteraceae). *Senecio viscosus*, one individual every 2.17 square metres, was more than twice as densely distributed as *Reseda luteola*, one individual every 5.5 square metres. Individuals from the group of common species, *Holcus lanatus, Centaurea nigra* and *Plantago lanceolata*, were recorded at one individual every 1- 0.4 square metres, more frequently distributed than four of the other species but less frequent than *L. vulgare*.

5.4.3 Seed production

Flower-head and seed production in each of the nine species varied considerably both between and within species (Table 5.3). The minimum counted seed production per plant in all nine species is between 0.2 - 5.6 % of the maximum counted seed production per plant. The potential maximum seed production was calculated by multiplying the highest count of flower-heads on any plant by the highest count of seeds on any flower-head and was always greater than the actual seed production. The difference between potential maximum and counted (actual) maximum numbers of seed produced by a single flower-head varied by less than 5% in *Centaurea nigra,* but was more than 80% in *Trifolium campestre*.

5.5 Results of trials

A series of glasshouse trials were set up as described in Section 5.3.3 to establish the viability of seeds within each of the nine species, measured as percentage germination success, and to ascertain the availability of all species in the seedbank, measured as the number of emerging seedlings from substrate samples.

5.5.1 Glasshouse germination trial

Germination rate was consistently higher in the five perennial species than the four annual species. More than 30% of the 240 sown seeds of *Leucanthemum vulgare*, *Reseda luteola*, *Holcus lanatus*, *Centaurea nigra* and *Plantago lanceolata* germinated successfully (Figure 5.7).

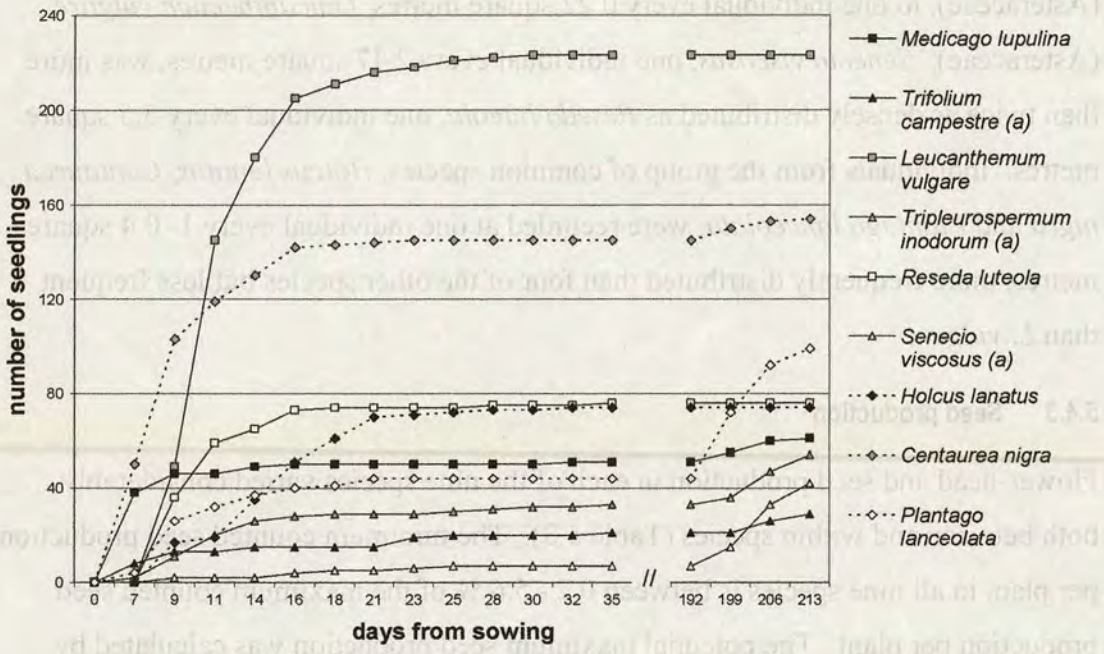


Figure 5.7 Germination trial

Two hundred and forty seeds of each species were sown in the mist room of the glasshouse on 11/10/99, day 0. The first seedling count was 18/10/99, day 7, then every Monday, Wednesday and Friday for seven weeks. The seed trays were moved to the cold frame and monitored weekly. // on the x-axis denotes a break in the displayed data when there was no germination recorded in any of the species (between 17/11/99 and 22/04/00). Germination continued on day 199 after a series of hard frosts toward the end of April 2000. There was no further germination after 13/05/00, day 213, although weekly monitoring continued until August. (a) after the species name highlights the annual species.

The germination rate in *L. vulgare* was very high, 93%, and all of the seeds that germinated did so during the initial 10-week period in the glasshouse. Successful germination of *R. luteola* (32%) and *H. lanatus* (31%) also took place completely within the early stages of the trial. Initial seedling emergence in all three of these species was slightly slower than for most of the others and the first seedlings were recorded on the ninth day after sowing although germination was very rapid over the following week. There was no further germination in the cold frame.

Germination in the remaining six species occurred both in the glasshouse and, after severe frost, in the cold frame. The two perennials displayed very different patterns of emergence. One hundred and three of the *C. nigra* seedlings emerged within nine

days and a further 42 in the first three weeks in the glass house. The remaining nine seedlings emerged in the cold frame resulting in a total germination rate of 64%. In contrast only 44 of the *P. lanceolata* seeds germinated in the glass house. The remaining 55 seedlings emerged rapidly after the frost resulting in a total germination rate of 41%.

As already mentioned germination success in the annuals was much lower. Thirty-eight of the germinable *Medicago lupulina* seeds germinated within the first seven days then germination was very slow for the remainder of the glass house stage of the trial. The frost-induced burst of activity six months later, in the following April resulted in a germination success of only 25%. *Trifolium campestre*, the other Fabaceae, was the least successful of the nine species with only 12% of seeds germinating. Many of these seedlings emerged within the first seven days but germination occurred in apparently random small bursts throughout the glasshouse stage of the experiment and the cold frame germination began a week later than the other species. *Tripleurospermum inodorum* also began to emerge within the first seven days and the rate of germination increased over the next two recording periods, then dropped to only occasional single seedlings. Further germination over the three weeks resulted in 23% germination success. *Senecio viscosus* had a very slow emergence rate in the glass house, only seven of the 240 sown seeds. A further 35 seeds germinated in the cold frame (18% germination success).

5.5.2 Soil seedbank trial

During the three-month observation period 514 seedlings from 46 species were identified and recorded. No ungerminated seeds were found in the samples at the end of the trial and there were no seedlings recorded in the control trays. Exactly 200 seedlings were from the nine species in this study (Table 5.4).

Holcus lanatus and *Plantago lanceolata* germinated from surface and unweathered samples at all three recording sites although *Centaurea nigra* was not recorded in any samples from any sites. *Leucanthemum vulgare* and *Reseda luteola* germinated in almost equal numbers from both the surface samples and from the unweathered substrate but the other species were more abundant in the surface samples. It should

be noted that all but one of the *L. vulgare* and *R. luteola* seedlings emerged from samples collected from Greendykes.

Table 5.4 Soil seedbank trial

The numbers of seedlings of each of the nine selected species germinating from 40 surface soil samples and 40 unweathered substrate samples (10 cm diameter and 5 cm deep) collected from each of the three bing sites are presented with the total number of seedlings of each species recorded and number of surface and unweathered samples containing the seedlings. The same data is presented for seedlings of other species and for all species emerging, including the nine, for comparison.

OB = Oakbank; CL = Clapperton; GD = Greendykes; sur=surface soil samples; unw = unweathered substrate samples

species	number of seedlings from surface soil			number of seedlings from unweathered substrate			total number of seedlings	number of samples with germinating seedlings	
	OB	CL	GD	OB	CL	GD		sur	unw
Medicago lupulina	1	0	0	1	0	0	2	1	1
Trifolium campestre	18	0	0	3	0	0	21	4	2
Leucanthemum vulgare	0	0	27	0	1	28	56	8	11
Tripleurospermum inodorum	0	3	0	0	0	0	3	3	0
Reseda luteola	0	0	12	0	0	11	23	4	3
Senecio viscosus	0	0	0	0	1	0	1	0	1
Holcus lanatus	15	10	3	5	5	2	40	8	9
Centaurea nigra	0	0	0	0	0	0	0	0	0
Plantago lanceolata	45	2	1	3	0	3	54	9	5
Other species	119	44	54	32	20	45	314	33	27
ALL SPECIES	198	59	97	44	27	89	514	34	31

Of the annual species, *Trifolium campestre* had the largest number of seedlings germinating from the seedbank with 18 seedlings sprouting from the surface samples and three from the unweathered substrate collected at Oakbank bing. Three seedlings of *Tripleurospermum inodorum* germinated from the surface samples collected at Clapperton bing and only two seedlings of *Medicago lupulina* germinated, one from the surface samples and one from the unweathered substrate collected at Oakbank bing.

The inter-specific variation in numbers and distribution of seedlings between the surface and unweathered samples was significant but there was no significant difference between the numbers of samples with germinating seedlings (calculating

χ^2 as described in section 5.3.6). There was also no significant difference between the combined total seedlings from the nine species and the seedlings from all other species between the surface and unweathered samples.

The overall seedling emergence was different in each of the three sampled bing sites (All species, Table 5.4). There were similar numbers of germinating seedlings in the surface and unweathered samples taken from Greendykes bing but recorded emergence was much higher from the surface samples than the unweathered substrate at Oakbank and Clapperton. The total number of species germinating from samples taken from Clapperton was significantly lower than from the other two sites (χ^2). However more complex statistical analyses of seedbank data such as these is not considered to be appropriate due to the very small counts of some species and the many zero values in the data (Bakker *et al.*, 1996).

5.6 Analyses of combined measurements and data collection

The data resulting from the field measurements and glasshouse trials were analysed in accordance with the methods described in Section 5.3.6. Correlations of the field and trial measurements were calculated between and within each of the nine species. The data were also analysed by Canonical Correspondence Analysis (CCA) in conjunction with the physical and chemical environmental data that was recorded from the fixed quadrats and analysed with all species distribution and abundance in Chapter Four (Section 4.5).

5.6.1 Correlations and calculations

Correlations between the field measurements of each species were expected to comply with the model: the taller the plant the more flower-heads; the more flower-heads the more seeds on each flower-head; the more seeds the greater the number of plants (population density); the greater the abundance the taller the plants (due to competition for light).

The correlations between measured data from *Tripleurospermum inodorum* plants exemplified this popular view of vigorous growth and copious seed production in pioneering or colonising species and show strong positive relationships between

these physiological measurements (Table 5.5). However none of the other species displayed all of these associations and a mixture of positive and negative correlations of varying scales was apparent for each of the paired data sets.

Table 5.5 Relationships between physiological measurements

The correlation coefficient was calculated for every combination of measured data collected in the 40 quadrat blocks from each of the nine species. The correlations highlighted in bold emphasise strong positive relationships.

ht = mean heights of individual plants; ab = numbers of individuals per quadrat block (population density); flo = mean numbers of flowering heads per plant; sd = mean numbers of seeds per flowering head.

species	ht:ab	ht:flo	ht:sd	ab:flo	ab:sd	flo:sd
Medicago lupulina	0.605	0.564	0.227	-0.612	-0.522	0.313
Trifolium campestre	-0.253	**0.771**	0.330	0.139	-0.052	-0.159
Leucanthemum vulgare	-0.555	0.671	-0.215	-0.240	**0.932**	-0.051
Tripleurospermum inodorum	**0.739**	**0.855**	**0.982**	**0.850**	**0.987**	**0.983**
Reseda luteola	-0.432	0.377	0.068	0.578	0.054	0.014
Senecio viscosus	**-0.949**	**0.958**	0.171	**-0.976**	-0.098	0.047
Holcus lanatus	0.468	0.480	-0.039	0.352	-0.357	**0.790**
Centaurea nigra	-0.664	**0.788**	-0.097	-0.092	-0.052	-0.122
Plantago lanceolata	-0.217	0.647	0.536	0.138	-0.262	0.079

The individual plant height to number of flower-heads ratio (ht:flo) showed a positive correlation in all nine species but this is likely to be a function of the modular growth plan of all vascular plants. None of the other ratios were consistently positive or negative for all nine species. For example *T. inodorum* plants were taller with increasing abundance but *S. viscosus* plants were smaller. There was little relationship between the number of flower-heads produced on each plant and the number of seeds produced on each flower-head on *Leucanthemum vulgare* and *S. viscosus* plants, yet on both *T. inodorum* and *Holcus lanatus* plants there was a strong positive correlation between these two sets of data.

The variation in measurements relating to seed ecology between species and between stages of development is summarised in Table 5.6. The loss of individuals at each stage of development is calculated by combining the results of field measurements and germination trials. There are clear discrepancies between the expected density of plants calculated from the germinable seedbank and the population densities recorded in the field.

Table 5.6 Summary of physiological results

Total seed production per m^2 (the sum of flowering heads x seeds per flower-head recorded in the field on each individual plant /640), germinable seed production per m^2 (percentage germination success in the glasshouse trial x total seed production), germinable seedbank per m^2 (extrapolated from the number of seedlings emerging in the seedbank trial) and density of plants per m^2 (from table 5.3.) have been presented for each of the nine species.

species	total seed production	germinable seed production	germinable seedbank	density of plants (measured)
Medicago lupulina	430	108	2	0.12
Trifolium campestre	108	13	21	0.15
Leucanthemum vulgare	2,546	2,368	56	4.49
Tripleurospermum inodorum	116	27	3	0.13
Reseda luteola	3,154	1,009	23	0.18
Senecio viscosus	224	40	1	0.46
Holcus lanatus	6,995	2,168	40	2.25
Centaurea nigra	1,835	1,174	0	2.66
Plantago lanceolata	297	122	54	0.96

5.6.2 Relationships to physical and chemical environment

Canonical Correspondence Analysis (CCA) of the individual components of the measured physiological data for the nine species (height, density, number of flower-heads and seed production) with physical environmental data was calculated with supplementary chemical environmental data. The influence of each of the environmental factors on the abundance of the nine species has already been demonstrated within the data for the most abundant species (Chapter Four, Figures 4.5 and 4.8).

The amount of explained variance in the CCAs of the physiological data with the same environmental factors ranged from 14% of the 14% variation in seed production, attributed to the chemical environment (< 2% explained variance), to 58% of the 66% variation in flower production, also attributed to the chemical environment (≈ 38% explained variance).

An exploratory CCA demonstrated that the percentage of explained variance was strongly influenced by the presence and absence of species within the environmental gradients. Variation of presence/absence in the species data was described by both

the physical (45.84%) and the chemical (32.84%) environmental variables and 45.3% of this variance was described by the first four constrained axes. The graphical display of the analysis as a triplot (Figure 5.8) presents the main influences of the physical environment on species presence or absence as bare ground and management and of the chemical environment as pH, sodium and potassium. The distribution of the nine species names on the triplot represents the extent that the presence or absence of each species is influenced by the environmental variables: for example *Tripleurospermum inodorum and Medicago lupulina* are positioned between the management and pH axes indicating that their presence is linked with both increased pH and management.

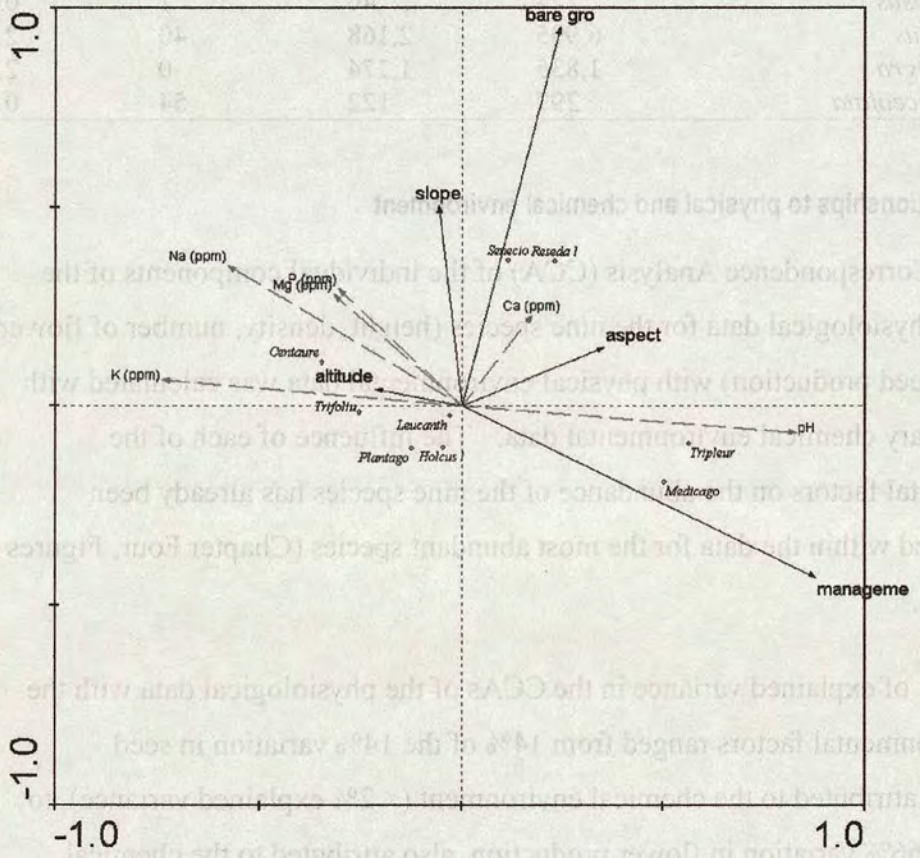


Figure 5.8 Triplot representing the CCA of species presence/absence with environmental variables

Because of the high percentage of variance in the species data that was explained by presence/absence the decision was made to repeat the analyses including presence/absence as a covariable within each CCA. The percentage of variance in the measured plant attributes that is described by the presence/absence covariable is unique to each of the analyses (Table 5.7). The inclusion of the covariable in the analyses reduces the percentage variance in the species data that is described by the environmental data (Phys% and Chem% in Table 5.7) by removing the effect of zero measurements when there were no representatives of a species present in the recording block. This change in emphasis can be demonstrated by comparing the triplot graphs of the CCA of the species flower-head matrix with environmental variables only (Figure 5.9) and with the presence/absence covariable included in the analysis (Figure 5.10).

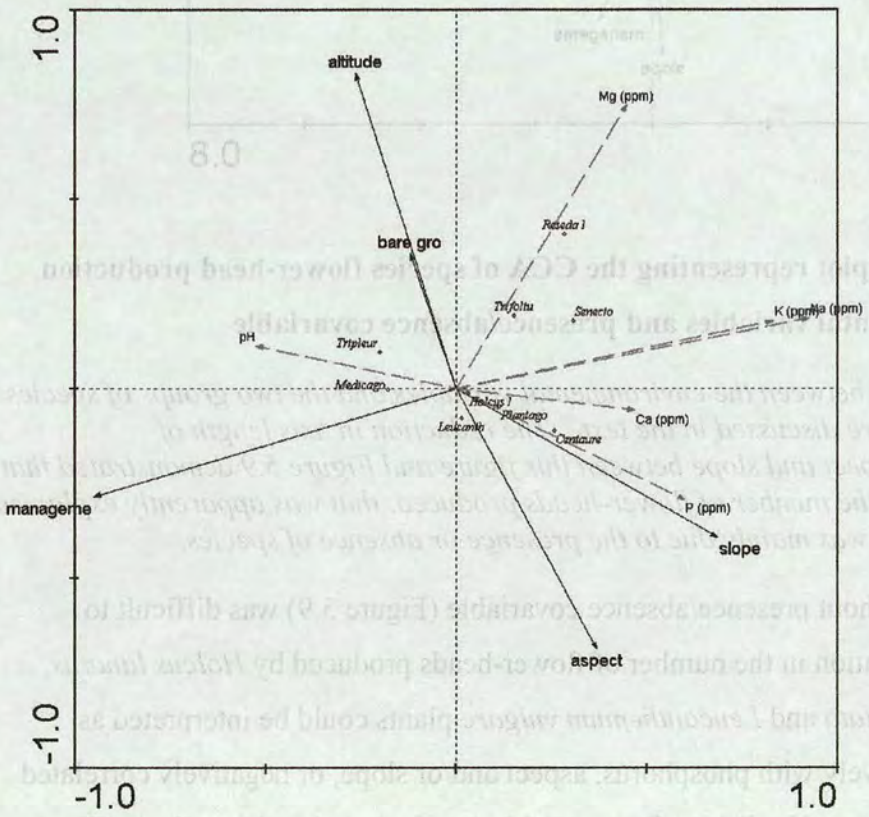


Figure 5.9 Triplot representing the CCA of species flower-head production with environmental variables

The relationship between this figure and Figure 5.10 are discussed in the text

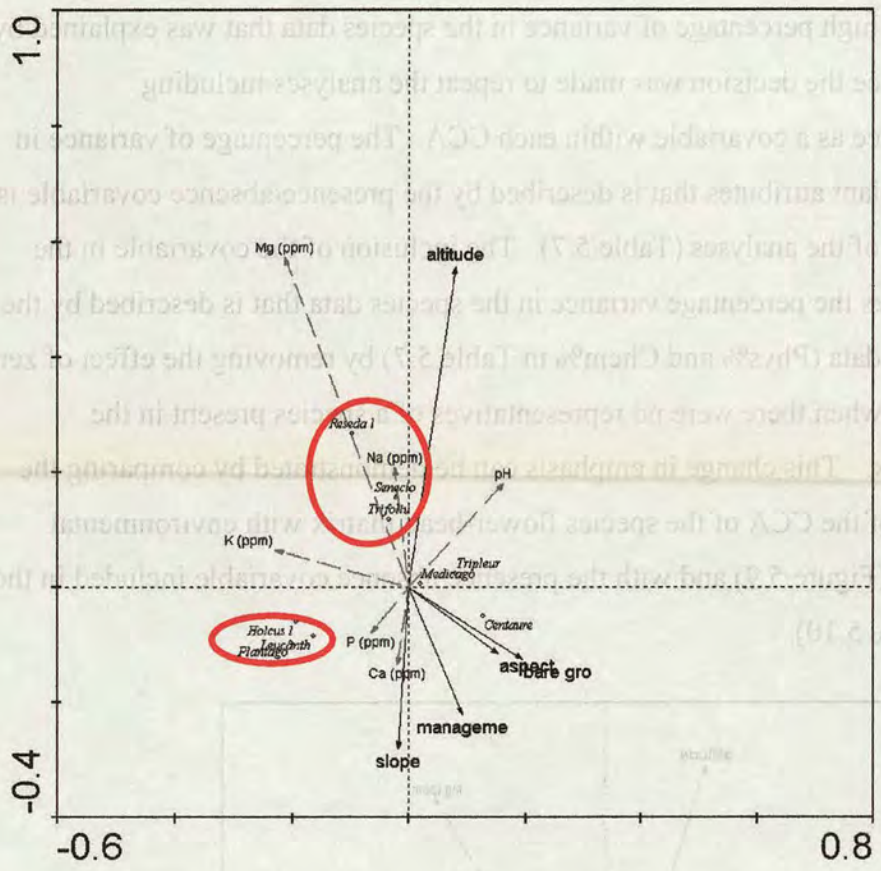


Figure 5.10 Triplot representing the CCA of species flower-head production with environmental variables and presence/absence covariable

The relationship between the environmental variables and the two groups of species circled in bold are discussed in the text. The reduction in axis length of management, aspect and slope between this figure and Figure 5.9 demonstrated that the variance on the number of flower-heads produced, that was apparently explained by these factors, was mainly due to the presence or absence of species.

The analysis without presence/absence covariable (Figure 5.9) was difficult to explain and variation in the number of flower-heads produced by *Holcus lanatus*, *Plantago lanceolata* and *Leucanthemum vulgare* plants could be interpreted as correlated positively with phosphorus, aspect and/or slope, or negatively correlated with altitude and/or pH. When the covariable was included in the analysis (Figure 5.10) these three species were grouped more closely together and the production of flower-heads was shown to be more clearly negatively correlated with the pH axis. Altitude and increased magnesium in the substrate were shown to correlate with increased flower-head production in *Reseda luteola*, *Senecio viscosus* and *Trifolium*

campestre both with and without the presence/absence covariable being included in the analysis. The log report of the CCA, produced by the CANOCO programme, confirmed that altitude (0.9249 correlation) and magnesium (0.6853 correlation) corresponded with the second constrained axis. The result of including the covariable in the analysis of flower-head production was to describe more than half of the variance in relation to presence of absence of species recorded in the quadrat blocks and in doing so reducing the amount of variance described by the physical and chemical environmental variables. The percentage of the variance that was now described in the first four constrained axes increased from 58.4% to 71.3%.

Increased heights in individual plants of the nine species were each correlated with different environmental factors. Plasticity (measured as variation in height) was linked to both the physical environment and the availability of nutrients. Interpretation of the CCA, without covariables, suggested that the height of *Medicago lupulina* plants was positively correlated with increased management and heights of *Holcus lanatus*, *Plantago lanceolata* and *Leucanthemum vulgare* plants were negatively correlated with altitude. However when the presence/absence covariable was included in the analysis the heights of *M. lupulina* and *H. lanatus* plants were now positively correlated, and of *Tripleurospermum inodorum* plants strongly negatively correlated, with calcium. More than 50% of the variance in height explained in the first analysis was apparently describing the presence and absence of species in the recording quadrats.

Variance in seed production was the least well explained by the measured environmental variables. A CCA of seed production with environmental variables including the presence/absence covariable suggested that variance in seed production in the nine species was not strongly correlated with any of the measured environmental factors and a comparatively low percentage of the variability was described. On reviewing the raw data the range of variation in numbers of seed produced both between and within species was noted (the highest counts were often more than 1,000 times greater than the lowest) and the decision was made to reanalyse the variables using the natural logarithm ($\log_n$) of seed numbers.

Transforming the data did not clarify the associations between seed production and the environmental variables.

In all of the analyses, both with and without the presence absence covariable, the first two constrained axes described most of the variance (Table 5.7). The variance in any of the species data that is explained by the environmental variables is the percentage variance calculated from the total inertia and eigenvalues given in the summary of results produced in the log (printed record) of the analysis (described in Appendix 16). The cumulative percentage variance is the amount of the calculated variance that is described by the first four constrained axes in the analyses.

Table 5.7 Summary of CCA results

The cumulative percentage variance gives the amount of variance explained by the first four constrained axes of the current environmental variables. The total inertia (the sum of the eigenvalues for the same four axes including any covariables), and the sum of all eigenvalues (EV) for only the environmental variables are used to calculate the percentage variance in the species data that is explained by the covariable (Cov %), the physical environmental variables (Phys %) and the chemical environmental variables (Chem %). A more complete explanation of the calculations and an example of analysis results are given in Appendix 16.

Species data	Cumulative percentage variance 1st axis	2nd axis	3rd axis	4th axis	Total inertia	Sum of all EV	Cov %	Phys %	Chem %
Presence absence	29.3	42.5	44.2	45.3	1.071	1.071	N/A	45.84	32.84
Height	22.8	38.0	40.3	41.1	0.953	0.953	N/A	41.44	43.55
Height + covariable	21.6	36.1	39.4	40.1	0.953	0.444	53.41	18.88	28.86
Flowers	41.1	52.8	56.6	58.4	1.330	1.330	N/A	58.96	65.86
Flowers + covariable	44.4	65.5	69.1	71.3	1.330	0.519	53.46	28.05	29.92
Seeds	13.2	14.0	14.1	14.1	2.769	2.769	N/A	14.08	18.02
Seeds + covariable	3.4	5.0	5.8	6.1	2.769	2.032	26.62	4.51	9.61
Log_n seed + covariable	8.4	11.5	13.2	14.4	2.278	1.431	37.18	9.35	17.47

5.7 Discussion and conclusions

The results from the field measurements and glasshouse trials demonstrated the inter- and intra-specific variation of the nine species and established that individual morphological features associated differently in each species. There is no simple model that can be established to describe the processes of reproduction, distribution and establishment of colonising species by extrapolating the information from these data.

5.7.1 Morphological measurements

The height ranges of individual plants in three of the species measured both significantly lower and higher than the published (Stace, 1997) usual ranges of height: *Leucanthemum vulgare*, *Reseda luteola* and *Plantago lanceolata*. Smaller plants are perhaps understandable, due to the inhospitable conditions on the surface of the bings, where there is no protection from the elements. Taller plants usually occur when there is competition for light or a nutrient rich soil. This has been demonstrated in tree species by King, (1991) and Koch *et al.* (2004). Variability in height in species growing on the bings may be an element of plasticity that is retained in early successional species to ensure that tall individuals, capable of more effective distribution, are available when environmental conditions are suitable. When flower-heads are positioned high on the plant, as they are in these species, the distance of dispersal of seeds from the adult plant is greater in a tall plant than a short plant. Carefully designed (and extensive) field trials would be required to establish the validity of this theory.

5.7.2 Germination trials

The germination trials produced results that were dissimilar to those reported in the much larger trials conducted by Grime *et al.* (1981). Although different experimental techniques were used to determine germinability in that study, the specimens were collected from similar substrates; limestone outcrops and disused quarries.

The total percentage germination and time to 50% germination (t_{50}) were compared with the findings of Grime *et al.* (1981) for 'germination of freshly collected seeds' of the nine species (Table 5.7). There were significant differences in either the total germination success or the number of days taken to achieve 50% of the successful germination (or both) in all species apart from *Leucanthemum vulgare*. The total percentages of successful germination in *Leucanthemum vulgare* and *Plantago lanceolata* were comparable with those recorded by Grime. The percentage of *Medicago lupulina* and *Centaurea nigra* seedling eruption was significantly higher in the trials conducted in this study. Conversely, successful germination of *Trifolium campestre*, *Tripleurospermum inodorum*, *Holcus lanatus* and *Reseda luteola* was significantly lower. *Senecio viscosus* germination appears to be much lower in the Sheffield study but the 1% success reported is for immediate sowing (without chilling) and is probably more comparable with the glass house section of my trial.

Table 5.8 Comparison of germination results

The germination results for the nine species recorded in this study are compared with those from the study of the Sheffield flora (Grime et al., *1981). The number of seedlings germinating from 240 seeds (Figure 5.7) is converted to percentage germination and t_{50} is the time in days required for 50% of the viable seeds to germinate.*

species	*Medicago lupulina*	*Trifolium campestre*	*Leucanthemum vulgare*	*Tripleurospermum inodorum*	*Reseda luteola*	*Senecio viscosus*	*Holcus lanatus*	*Centaurea nigra*	*Plantago lanceolata*
total germination (%)	25	12	93	23	32	18	31	64	41
published germination (%)	5	72	92	72	80	1	100	36	37
t_{50} (days)	<7	15	12	17	12	>200	17	10	>200
published t_{50} (days)	7	5	8	21	4	>200	3	35	14

The times to 50% germination (t_{50}) for seeds of *T. inodorum*, *L. vulgare*, *S. viscosus* and *M. lupulina* were comparable with the Sheffield study. Germination of

T. campestre, *R. luteola*, *H. lanatus* and *P. lanceolata* seeds was significantly slower than reported and *C. nigra* seedlings emerged more rapidly. *P. lanceolata* emergence from the bing substrate was more successful after the April frost.

The double germination pattern of six of the nine species, the species in the trials from this study, could have been examined as two separate germination events and would have made the results more comparable with the Sheffield study but would not be so representative of field conditions, which are ultimately what is being simulated. The combined trial with a single cohort of seeds demonstrates that within a single growing season there are species, like *Plantago lanceolata*, that produce some seeds with the inherent plasticity to germinate immediately while the non-germinating seeds remain dormant until particular stimuli are received (in this case severe chilling). Other species produce seeds that are all 'programmed' for immediate germination. In this study these were not annual species and the most extreme example was *Leucanthemum vulgare* with 93% germination from freshly sown seeds (a finding comparable with Grime *et al.*, 1981). Yet other species produce seeds that remain dormant until activated by a stimulus other than cold. The sporadic germination of *Trifolium campestre* seeds possibly exemplifies this last mechanism.

The lack of similarity between individual species in the two sets of trials (this study and Grime *et al.*, 1981) could be linked to differences in the provenances of the seeds being used. Mkonda *et al.* (2003) demonstrated that cumulative germination percentage differed significantly between provenances in seeds of *Strychnos cocculoides*, a wild indigenous fruit tree of Zambia.

In addition climatic conditions in central Scotland and the Sheffield area are quite different and this alone could lead to plants producing seeds that respond to different germination stimuli. Mean climate data over the 30 years from 1971 – 2000 show that, in comparison with Edinburgh, Sheffield has 20 fewer days of frost annually, higher minimum and maximum temperatures throughout the year, and higher rainfall and more rain days every month of the year except July (Meteorological Office, 2004a; 2004b).

The simple germination trial of this study could be replicated using seed collected from cohorts of the same species growing in the same sites in different years or using seeds collected from cohorts of the same species growing in different conditions (Cornwall and Caithness for example) in the same years. The resulting information would give a clearer understanding of the extent of plasticity and variability in this one small contributing factor to species distribution. Many of the experimental conditions produced in the Sheffield trials are not representative of normal field conditions in either Sheffield or central Scotland (e.g. dry storage for 3 and 6 months, or moist storage at 20°C). There is, however, potential for more, detailed trials on the effects of moist storage at lower temperatures on the germination of seeds.

5.7.3 Seedbank trials

The total number of seedlings, from all species, emerging from the seedbank on the bings was very low compared to numbers recorded in abandoned wet meadows by Jensen (1998); however the literature suggests that these results are an accurate representation of the seedbank. The bulking of samples increased the likelihood of species being represented in the sample. Reduction of substrate bulk is recommended in seedbank analysis as the number of species emerging is higher in concentrated samples and the process of reduction scarifies the seed coats (ter Heerdt *et al.*, 1996; Thompson *et al.*, 1997). Traba *et al.* (1998) suggest that there may be a loss of species with seed diameters less than 0.2 mm in concentrated samples and although this may prevent a few of the total number of species germinating from the seedbank it should not affect the volume of emergence from the nine species in this study as their seeds all have a larger diameter (even *R. luteola*).

Glasshouse experiments have been shown to result in higher germination rates than field trials for arable weeds (Roberts & Ricketts, 1970; Graham & Hutchings, 1988) and it would have been advantageous to replicate the germination trials in the field. Unfortunately the agreements to carry out research on the bings precluded manipulative experiments or *in situ* trials. Only Seafield, which has also been utilised as a landfill site (Appendix 1), could have been used for this purpose but was not comparable with any of the other bing sites.

More than half of the seedlings that emerged from the Greendykes samples grew from the unweathered substrate, 5 cm below the surface. This appears to confirm that some species, particularly *Leucanthemum vulgare* and *Reseda luteola*, can persist through enforced dormancy when seeds become buried. A key feature of seedbanks is the ability of seeds from some species to survive in a dormant state for 20 years or more until conditions for germination are suitable; indeed Ramsbottom (1942) describes the germination of an herbarium seed that was known to be 237 years old. Thompson *et al.* (1997) make a general inference that seeds buried at depth are older than seeds on the surface and represent non-transient seed banks, a suggestion that seems to be supported by the evidence collected from the nine selected species in this study. Despite four of the nine species being annuals only *Tripleurospermum inodorum* was recorded solely from surface samples suggesting that a persistent seedbank may be retained in the bing substrate. This theory could be investigated further using the data collected for other species germinating from the samples and comparing them with the above ground vegetation data, however the coarse structure of the bing substrate must also be taken into account as it will allow all but the very largest seeds to be washed between the shale particles, probably to considerable depths.

5.7.4 Multivariate analyses

Morphological variation and seed production between and within species was explained in relation to the physical and chemical environment in a series of Canonical Correspondence analyses. Once the confounding influence of presence/absence was removed from the analyses it became clear that the variance in height, flower production and seed production of each of the nine species was explained by different environmental variables.

There was a positive correlation between the height of *Medicago lupulina* and calcium yet this species was consistently measured at less than 50% the published height (Stace, 1997). There were no quadrats where available calcium was measured as deficient in the substrate (Bradshaw and Chadwick, 1980) that might explain lack of growth. The species is acknowledged to be recorded most frequently in alkaline

soils (Hill *et al.*, 1999) and conditions on the bing substrate are alkaline. *Tripleurospermum inodorum* plants were also consistently smaller than the published expected height but the height of this species is negatively correlated with calcium. It would be imprudent to emphasise the importance of this information however as less than 11% of the total variance in height of all nine species is explained by the combined influence of the six measured variables of the chemical environment.

The comparatively high percentage of explained variance in flower production was unexpected and some of the correlations with environmental variables were very strong. Increased flower production in *Reseda luteola, Senecio viscosus* and *Trifolium campestre* plants was positively correlated with magnesium, sodium and altitude but negatively correlated with management. In *Holcus lanatus*, *Leucanthemum vulgare* and *Plantago lanceolata* plants flower production was negatively correlated with pH and positively with potassium and phosphorus, but the opposite was true of *Tripleurospermum inodorum* and *Medicago lupulina* plants. Increased flower production in *Centaurea nigra* plants correlated positively with increased bare ground and negatively with potassium. Fabbro and Korner (2004) documented a decrease in the number of flowering heads produced by individual plants, with increased altitude in alpine habitats: a relationship that was not evident in this study, possibly due to the comparatively limited variation in altitude on shale bings.

The seemingly strong influence of the environment on flower production in all nine species made the lack of explained variance in seed production by the measured environmental variables difficult to interpret. In some instances a variable that had a positive correlation with flower production had a negative correlation with seed production in the same species or *vice versa*: for example magnesium, positive for flower production and negative for seed production in *Trifolium campestre,* and phosphorus, negative for flower production and positive for seed production in *Tripleurospermum inodorum.* The lack of strong positive correlation between number of flowering heads and numbers of seeds produced was demonstrated earlier in this chapter but does not explain the anomaly of a single environmental factor having apparently opposing effects on the fecundity of a species.

I can find no references from literature that either support the findings from these analyses or offer alternative theories for the causes of the extreme vagaries of within and between species physiology in these nine species.

5.7.5 The nine species

The two Fabaceae were selected because despite their similarity of physiology and habitat requirements, they were not recorded together on the bings. The two species were measured at similar overall population densities on the bing sites but the relationship between the other measurements recorded from the two species was very different. The height of *M. lupulina* plants increased with abundance while the number of flower-heads and number of seeds per flower-head both decreased but there was little correlation between the same measurements in *T. campestre* plants.

The presence of *Medicago lupulina* in the seedbank of both the surface soil and unweathered substrate at Oakbank was not anticipated, as it was not recorded as a surviving plant in any of the quadrats from this site. There must be, or have been, a local seed source, perhaps the surrounding agricultural land. Pavone & Reader (1982) found that seedbank size in *M. lupulina* ranges from a few tens per m^2 to several thousand, depending on topography, habitat and past history. Reader (1993) recorded that predation in or on the ground accounted for the loss of 80% of *M. lupulina* seeds in abandoned pasture. While this may go some way towards explaining the lack of recorded plants at Oakbank it does not fully explain the absence of germination from the substrate samples of sites where *M. lupulina* plants were producing plentiful, viable seed. Some factor(s), not considered in this investigation, is preventing the germination or establishment of this species.

Trifolium campestre was found in high numbers in the seedbank, compared to the other annual species, and only at Oakbank. It was recorded in both the surface soil and the unweathered substrate so can be considered to be persistent on this site. The germination density in the seedbank trial was higher than that expected from the results of the germination trial. It is possible that the apparently random bursts of germination noted in the trial continue throughout the year as a response to different

stimuli and that the potential germination for this species was under recorded as a result.

Leucanthemum vulgare and *Tripleurospermum inodorum* were also selected as a pair of species, similar in appearance and from the same family. The glasshouse trials established that over 90% of *Leucanthemum vulgare* seeds, collected from seedheads, germinated immediately with no further germination after chilling, indicating an absence of any innate dormancy. Grime *et al.* (1981) reported similar results (90-100%) in their trials. The recorded density of this species in the field is high, but this is not unexpected as *L. vulgare* is a perennial species that persists above the ground rather than below and is also more competitive than many other species. These strategies allow sustained survival in undisturbed sites.

Fenner *et al.* (2002) demonstrated that, for both *L. vulgare* and *T. inodorum*, predation on the seeds in the capitulum increases with size of capitulum and that *L. vulgare* consistently has larger capitula (an observation supported by the measurements in this study). Studies of the two species in populations from grassland, arable fields and waste ground in Hampshire (Fenner *et al.*, 2002) revealed that percentage insect infestation suffered by *T. inodorum*, 33% (±12.3), is higher than the 26% (±11.8) recorded in *L. vulgare*. The authors have assumed that seed infestation is synonymous with predation. Post-dispersal seed predation is also very high for many species. In a study of abandoned pasture Reader (1993) suggests that up to 93% of *L. vulgare* seeds may be lost to predation when in or on the ground.

A combination of the two types of predation would considerably reduce the number of seeds being retained in the seedbank and may explain the apparent lack of seeds in the seedbank trials. The 93% losses to predation presented by Reader (1993) would reduce the *L. vulgare* potential seedbank from 2,546 per m^2 (mean seeds produced) to 16 per m^2 (seeds remaining after pre- and post-dispersal predation), considerably closer to the actual density of plants recorded in the field than germination and seedbank trials would infer. *Tripleurospermum inodorum* seedlings emerged only from surface soil samples. Although the numbers of individuals recorded are small, this suggests that either the species has colonised the area recently, such that the

seeds have not yet been moved through the spaces between particles in the substrate, or that it is a transient species as described by Thompson *et al.* (1997). The species is certainly recognised as a ruderal that is often found in cultivated ground (Smith *et al.*, 2002) and a requirement for high levels of disturbance may limit its distribution on the bings and explain why it is not recorded consistently with any of the other species.

Reseda luteola and *Senecio viscosus* were two unrelated species apparently sharing the same ecological niche and abiotic resources. Both species are strongly linked with a high percentage of bare ground suggesting that they are not in competition for any resources. They also represent the mixture of longer-lived and shorter-lived pioneers that are common to shingle banks (Scott, 1963; Grubb, 1987). On the bings *Reseda luteola* and *Senecio viscosus* were representative of the vegetation on a scree-like habitat that is not found in the surrounding landscape. *S. viscosus* is a 'conventional' short-lived, annual, pioneer species whose appearance on the bings reflects a strong association with man-made sites and transport routes. There is considerable debate as to whether it is native. Smith *et al.* (2002) record the species as native, Stace (1997) states that it may be native and the New Atlas (Preston *et al.*, 2002) suggests that the species is not native, except perhaps as a genetic dwarf form on coastal shingle. As previously noted, the specimens on the bings were consistently smaller than the expected normal range of height and the comparatively isolated examples on the bings may be genetically allied with the coastal shingle variants. Unfortunately Preston *et al.* (2002) do not define the native distribution. The very strong negative correlation between height and abundance, and positive correlation between height and number of flower-heads found in *S. viscosus* plants recorded on the bing sites may be indicative of a restricted gene pool caused by a combination of isolation and apomixis.

R. luteola is a longer-lived biennial whose native status is also debated. The seeds of this species are dispersed by wind, although they are released from capsules then roll along the ground rather than being dispersed through the air over long distances (Hodgson *et al.*, 1995). Again it has strong associations with man-made sites but exactly how the seeds travel from one site to another is not clear. The measurements

recorded in this study showed no strong correlation in *R. luteola* although individuals demonstrated a larger than expected plasticity of height (Stace, 1997). *R. luteola* produced more than ten times as many seeds as *S. viscosus* and more of the seeds germinated from the seedbank in trials yet the population density of plants on the bing was much lower. Predation must play a considerable part on the survival of both seeds and seedlings, as it does in other species, and lack of suitable microsites for establishment may also be a contributing factor but I was unable to find any definite information on either of these species in the literature.

The three species selected because they are very common on both the bings and a wide range of surrounding habitats, *Holcus lanatus*, *Centaurea nigra* and *Plantago lanceolata,* are all perennials. *H. lanatus* and *C. nigra* were both demonstrated to be extensive producers of seed from this study (Table 5.3). *H. lanatus* produces large numbers of seeds in each flower-head and *C. nigra* produces large numbers of flowers on each plant. *P. lanceolata* is less productive than the other two species and this is reflected in the lower density of plants but was shown to have a high success rate in the germination and seedbank trials. High seed production and germination success, combined with vegetative regeneration and longevity, leads to the high density of plants, in all three species, recorded on the bings. The same factors are probably responsible for the general abundance of these species throughout Britain.

The apparent absence of *C. nigra* in the seedbank of all three sites in this study was unpredicted. The large number of seeds produced in the field and high germination rates in the glass house trials suggest that there should be a noticeable presence of this species in the seedbank. Seeds tend to be retained in the head of this species and are shed at irregular times throughout autumn and winter. The seeds are known to be heavily predated both by insects, in the capitula, and small rodents, on the ground (Grime *et al.*, 1988) although Fenner *et al.* (2002) recorded a much lower percentage of insect infestation in this species compared with the two Asteraceae species (12.7 ± 4.0). *C. nigra* may rely more heavily on longevity and permanence of individuals on the bings than the other species.

Individuals of *P. lanceolata* were recorded in the field at almost twice the published normal maximum height of 500 mm (Stace, 1997). Height was not correlated with any of the measured environmental factors but particularly tall individuals with additional leaf rosettes on the scape and multiheaded forms were recorded at Oakbank. There is some debate as to whether this unorthodox development is genetic or caused by galls but it is not normally associated with increased height (Cragg-Barber, 1999). Plants with this aberration were consistently found in close proximity to phyllodic clover and the two species could form the basis of an innovative, teratological investigation.

5.7.6 General observations

This chapter set out to address a series of questions that would help to explain some of the variance in species distribution on the shale bings that had not been associated with physical or chemical environmental gradients and to determine the roles of inherent plasticity, seed production, seed persistence and seedbank in the observed distribution of nine common weed species on shale bings.

In all nine species there is a massive discrepancy between the potential for seedlings, measured as germinable seed produced per m^2 and the density of plants recorded in the field. This suggests high seed and seedling predation or mortality through other causes. Pre-dispersal seed predation by insects has been shown by Reader (1993) to be responsible for up to 90% of seed loss and a similar percentage of seeds are lost to rodents post-dispersal although these percentages vary considerably between species.

The unsuccessful seed rain trials and resultant lack of data from the seed traps was unfortunate especially in the light of the apparent inconsistencies in seed losses between the stages of seed development in all species. A range of alternative seed trap designs were considered before finally adopting the seed traps described in section 5. Many of the commonly used seed trap designs have been developed for use in forestry and are large and noticeable structures that are impractical for use in open habitats, like the shale bings, that are well-used by members of the public. In addition there are intentional biases in the designs to favour the trapping of tree seeds: small and wind-blown seeds when using sticky traps and bird dispersed seeds

when using bucket traps (Kollmann and Goetze, 1998). The design adopted in this study was an adaptation of Schott's (1995) seed trap and was selected because it was low lying and inconspicuous, inexpensive and minimised predation (allegedly).

The collection of quantitative data on the composition of seed rain on the shale bings should be attempted in future studies when a new, crow-proof, seed trap design has been developed and tested in the field. In addition to providing results that could be compared with seed trap trials from literature and objective data to support (or refute) the published seed loss from predation, future analysis of seed rain collections could be used to differentiate between locally produced seed from incomers using genetic markers. For example information on the provenance of the *Senecio viscosus* plants recorded on the bings could provide evidence that would establish if these very small plants are examples of the native dwarf variety alluded to by Preston *et al.* (2002).

There has been a strong inference in this chapter that successfully germinated seedlings will ultimately become mature plants. Seedling mortality on the shale bings has not been considered in the explanation of loss of individuals between seed production and numbers of mature plants recorded in the field and is probably extremely high. Exposure and desiccation are only two obstacles that seedlings have to survive. Abiotic factors like these are likely to have a greater influence on the distribution and abundance of colonising seeds and spores than biotic factors. Jumponnen *et al.*, (1999) cite microsites with concave surfaces, coarse surface substrate and those in the vicinity of large rocks as most likely to entrap available seed but the microsites where seeds are trapped must be conducive to germination. The sparse cover of vegetation on many parts of the bings makes them ideal sites for further investigation into the effects of microclimate on seedling survival by comparing surfaces that have and have not been invaded.

The weak correlations between the measured factors of the physical and chemical environment and the variations in height and seed development of the nine species warrant further investigation. It was expected that data collected from these nine common species would indicate that morphology and productivity follow a pattern, or patterns, relating to nutrient availability or physical environment that reflects

stages of soil development and would therefore go some way towards explaining the variance in distribution of vegetation generally. The nine species have demonstrated different relationships between abundance, plant height, number of flower-heads produced and number of seeds produced and the results of the multivariate analyses suggest that the measured environmental factors are influencing the physiology of each species independently.

It must be stressed, however, that although these relationships can not be extrapolated to produce a model for all species in all habitats the analyses of the data demonstrated that the productivity and dispersal mechanisms in each of the nine species studied are significant factors in their distribution (Section 5.6.1) and that almost half the variance in distribution patterns is explained by a combination of physical and chemical environmental factors (Section 5.6.2).

5.7.7 Conclusions

There were almost unlimited interesting issues that could be developed from the data already collected from this study and several of these have been proposed for future investigations throughout this and the preceding chapters. Many factors have not been taken into account in the investigation of the nine species. Above ground morphology expressed as longevity, vegetative spread and persistence are additional properties of perennial plant species that are important in determining relative abundance (Mitchley and Grubb, 1986) and the plasticity within these species is expected to reflect nutrient availability (Grubb, 1987). Annual ruderals may reproduce quickly enough and with sufficient genetic variation to adapt to the non-optimal conditions found on the bing surface within a few growing seasons. The effects of competition, both above and below ground, may have a greater influence on the distribution of species than expected from the sparse vegetation and large expanses of bare substrate recorded on the bings. Unfortunately there were insufficient resources within the remit of this PhD to expand these hypotheses and questions.

The studies have determined that availability of seeds and methods of dispersal are a major determining factor in the establishment of vegetation on the bings. The field

measurements, trials and analysis have established that the height of individual plants within the nine selected species and also the numbers of flowers heads and seeds produced are directly affected by local site conditions. Almost half of all of the variance in physiology in the nine species can be explained by the variables of physical and chemical environment that were measured in this study. The phenotypic plasticity and mechanisms of productivity in each these species respond to different elements of the environment making it impossible to create a generic model of all species. However the study has determined the range of variance that can be expected in plant height, flower and seed production and the percentage of variance in each of these that is explained by one or more of five physical and six chemical environmental variables for each of nine common plant species selected from 211 species growing on the oil-shale bings.

If every one of the species recorded in the baseline survey was researched in the same detail as the nine selected species the combined information collected would be unlikely to provide any ecologically significant additional information on vegetation dynamics. Instead of delving more deeply into the minutiae of individual species the decision was made to take a more holistic approach by modelling the mechanisms and processes of the successional progression on the bings that have been discussed in this and earlier chapters and comparing them with other successional sites, both natural and man-made. A model based on the findings of this thesis would also establish whether the colonisation of the bings follows the accepted models of succession from literature.

CHAPTER SIX

"This plant is the first that vegetates on naked rocks, covering them with a kind of tapestry and draws its nourishment perhaps chiefly from the air; after it perishes, earth enough is left for other mosses to root themselves; and after some ages soil is produced sufficient for the growth of more succulent and larger vegetables. In this manner perhaps the whole earth has been gradually covered with vegetation, after it was raised out of the primeval ocean by subterraneous fires."

Erasmus Darwin (1789) *The Botanic Garden.* Part II. The loves of plants. J.Moore, Dublin.

6 Successional Models and Other Primary Sites

This chapter compares the mechanisms and processes of vegetation succession in the bing habitat as observed and measured in this study with examples from literature of successional models and the development of vegetation on other primary sites.

In earlier chapters the causal mechanisms and processes of vegetation dynamics on oil-shale bings have been discussed in relation to various spatial scales: the combined data from all bing sites, the individual bing sites, positions over all sites, positions-on-site and individual quadrats. In Chapter Three classification and ordination established that there were recognisable patterns in the vegetation and in Chapter Four the plant communities within and between the shale bings were associated with physical and chemical environmental gradients. Nutrient availability and lack of competition were established as determining factors in many species associations as was the availability of suitable sites.

Having established some of the mechanisms and processes producing the patterns in vegetation on the shale bings, a more detailed investigation was made using individual species. A series of trials established the complexity of variations in their physiological traits (Chapter Five) and identified the importance of seed production and dispersal as major contributors to the outcome of succession.

The aims of this chapter are to produce a model of the succession patterns on the bings that can be compared with models of succession from the literature and to test whether the plant species strategies and dispersal processes recognised in the primary succession of vegetation on oil-shale bings are similar to those found on other primary succession sites, both natural and man-made by addressing the questions:

Do bings provide acceptable models of primary succession?

Does succession on shale bings follow previously identified 'rules'?

Do the patterns of succession follow the same trends as those recorded on other primary sites, both natural and man-made?

Does the vegetation on oil-shale bings develop in an analogous way to other island communities, particularly those found on volcanoes and oceanic islands?

6.1 Primary Succession on Bings

A conceptual model of vegetation succession on the oil-shale bings of West Lothian was constructed using the vegetation data collected in this study and the results of the trials to formulate a sequence of early and later seral stages of primary succession on shale bings, both temporal and spatial. The model describes colonisation by plants on shale bings from the date of cessation of dumping. The bings are potentially an inhospitable habitat where establishment of vegetation is affected by steep slopes, altitude and a substrate that differs both chemically and physically from the surrounding area.

6.1.1 A model of bing succession

The model is constructed with a combined hierarchical and modular structure based on the ModMED modelling environment (Legg *et al.*, 1998). The structure of the model allows succession to be described at several levels, reflecting the different scales of processes and mechanisms determining vegetation dynamics, from region to individual plant (Figures 6.1 and 6.2). Several of the individual species modules can be represented within each of the community modules: these symbolise the numbers and diversity of seeds invading from the surrounding landscape. Equally several of the community level modules can be represented within each of the landscape modules: these symbolise the effects of within site variation in physical

and chemical environment on the germination and establishment of the invading species (Legg *et al.*, 1995). Finally at the landscape scale the influence of the size of individual sites, particularly altitude and aspect, on the distribution of invading species produces a vegetation map of the bings within the surrounding countryside.

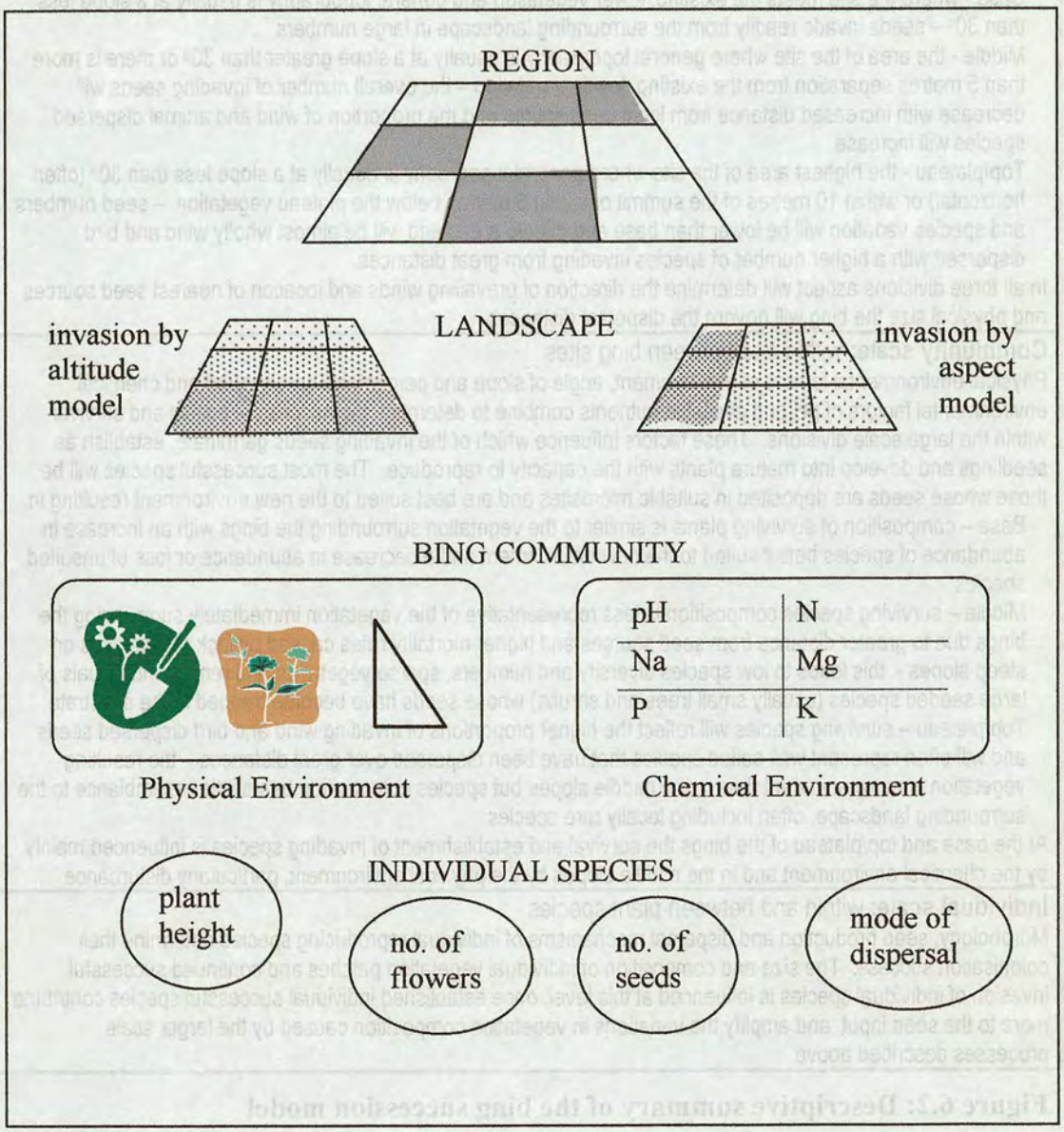


Figure 6.1 The hierarchical and modular structure of the bing succession

The development of different hierarchical levels each with modular components allows variation within modules at landscape level to be described by several alternative bing community level models. In addition several different individual species models can be represented within the same bing community. Adapted from Legg et al. *(1998)*

Regional scale: the county

The vegetation map of West Lothian. The physical environmental factors of bing size, basal area, height and aspect determine rates of invasion from seed sources in the surrounding countryside. Their effect varies between bings reflecting distance from existing vegetation and the efficiency of dispersal mechanisms and seed production of individual species in other habitats to reach the bare substrate

Landscape scale: between bing sites

The bing sites are modelled in three divisions according to physical structure:

Base - where the site meets the existing, lower vegetation and general topography is usually at a slope less than 30° – seeds invade readily from the surrounding landscape in large numbers

Middle - the area of the site where general topography is usually at a slope greater than 30° or there is more than 5 metres separation from the existing, lower vegetation – the overall number of invading seeds will decrease with increased distance from local seed source and the proportion of wind and animal dispersed species will increase

Top/plateau - the highest area of the site where general topography is usually at a slope less than 30° (often horizontal) or within 10 metres of the summit or within 5 metres below the plateau vegetation – seed numbers and species variation will be lower than base and middle areas and will be almost wholly wind and bird dispersed with a higher number of species invading from great distances

In all three divisions aspect will determine the direction of prevailing winds and location of nearest seed sources and physical size the bing will govern the dispersal distances

Community scale: within and between bing sites

Physical environmental factors of management, angle of slope and percentage bare ground and chemical environmental factors of pH and available nutrients combine to determine the success of ecesis and survival within the large scale divisions. These factors influence which of the invading seeds germinate, establish as seedlings and develop into mature plants with the capacity to reproduce. The most successful species will be those whose seeds are deposited in suitable microsites and are best suited to the new environment resulting in:

Base – composition of surviving plants is similar to the vegetation surrounding the bings with an increase in abundance of species better suited to the new environment and a decrease in abundance or loss of unsuited species

Middle – surviving species composition is less representative of the vegetation immediately surrounding the bings due to greater distance from seed sources and higher mortality rates caused by lack of safe sites on steep slopes - this leads to low species diversity and numbers, sparse vegetation and remote individuals of large seeded species (usually small trees and shrubs) whose seeds have become trapped in the substrate

Top/plateau – surviving species will reflect the higher proportions of invading wind and bird dispersed seeds and will often represent well suited species that have been dispersed over great distances – the resulting vegetation is more abundant than in the middle slopes but species composition bears little resemblance to the surrounding landscape, often including locally rare species

At the base and top/plateau of the bings the survival and establishment of invading species is influenced mainly by the chemical environment and in the middle slopes by the physical environment, particularly disturbance

Individual scale: within and between plant species

Morphology, seed production and dispersal mechanisms of individual reproducing species determine their colonisation success. The size and composition of individual vegetation patches and continued successful invasion of individual species is influenced at this level: once established individual successful species contribute more to the seed input and amplify the variations in vegetation composition caused by the larger scale processes described above

Figure 6.2: Descriptive summary of the bing succession model

The vegetation succession of the bings is summarised in terms of region, landscape, bing community and individual plants. The smaller scalar levels describe mechanisms and processes within, and contributing to, the large-scale processes. Adapted from Legg et al. *(1998).*

6.1.2 Describing the bing succession

The model simplifies the complex series of mechanisms and processes that are interacting at each spatial and temporal level of the bing succession. A more detailed description of the succession was compiled: predominantly from the data collected in the baseline survey and giving more weighting to evidence collected from the unmanaged sites as these were considered to be more representative of natural invasion.

Originally the whole surface of the bing substrate was totally barren and contained no organic matter; the same is true for many other industrial waste sites. On the bings the unweathered shale has been deep mined and heated to 500° C making it completely sterile: there are therefore no organisms, spores or seeds in the substrate. The blue substrate of unweathered shale (blaes) can now only be seen after a landslip or when other major disturbance reveals the anaerobic layers of subsoil, and is the colour of newly dumped material. The shale weathers rapidly and the characteristic red of weathered shale (red blaes) is the colour usually associated with the shale bings. The change in colour is caused by oxidation of elements in the substrate when they are exposed to oxygen and moisture in the air.

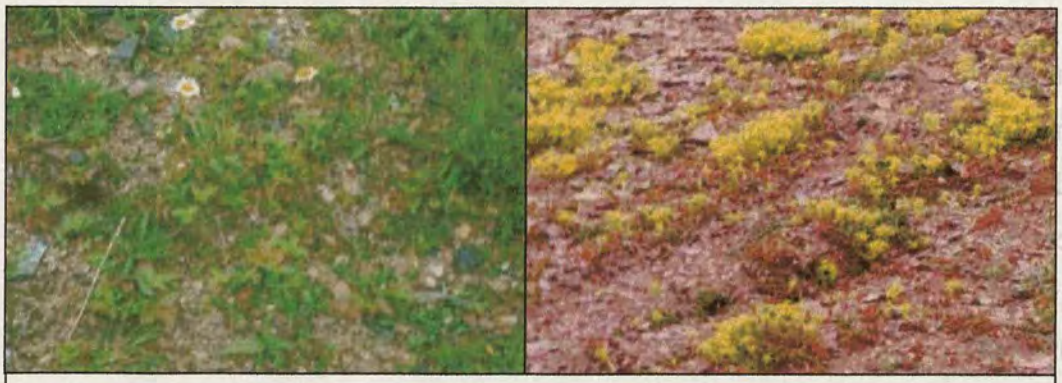
Initial invasion is stochastic: individual plants developing from available seeds wherever they fall and most representing species from the surrounding agricultural and urban landscape. Near neighbours from local sources make a greater contribution to the seed rain than more distant seed sources and have an increased probability of colonisation. The numbers of seeds produced by individual plants, the abundance of the species and dispersal mechanisms all affect the amount and composition of the seed rain. With increased distance (both length and height) from the source, the total numbers of seeds decrease while the proportion of wind and bird, or other animal, dispersed seeds increase. This combination of events and processes is theoretical as no data were collected from seed trapping in this study. Locally abundant species, like *Vicia cracca* and *Achillea millefolium*, that are limited in distribution to the lower slopes of the bings, even after more than 50 years of succession demonstrate that most seeds produced are deposited very close to the

parent plant however, and only a small proportion of seed from the surrounding landscape will be carried beyond the lower slopes of the bings to the middle slopes and summits of the bings.

Vegetation builds up around the pioneering individuals that first invade the site, and as plants become established and reproduce the seed rain gains a second component from seed produced within the site. In-site seed production is expected to remain the secondary seed source for many years because the vegetation remains sparse (Urbanska *et al.*, 1998) nonetheless it determines the rapid incursion of individual species like *Reseda luteola*, *Senecio viscosus* and other transitory species that are rare in the surrounding landscape but suited to the bing environment. The result of these processes is evident from the patchiness of invasion, particularly the mosaic of vegetation interspersed with large areas of bare substrate after more than 50 years of colonisation on the unmanaged bing sites, and are the main cause of the variation in species composition between the base, middle and upper sections of the sites.

At the base of the bing the seed rain is expected to reflect species composition and abundance, plus seasonal fluctuations in seed production, of existing near neighbours in the local vegetation as described in the previous paragraph. The composition of surviving plants is similar to the local vegetation with an increase in some species that are better suited to the new environment and a decrease or total loss of species that are unsuited. Common agricultural escapes, like oil-seed rape, that are commonly recorded on road verges and other disturbed ground throughout the county have not been recorded even on bings that are surrounded by this crop. Species diversity and abundance is high in comparison with the rest of the bing site. When the spatial distribution of established seedlings is clustered to the extent suggested by the theories for invasion, germination and establishment presented in Chapter One (section 1.4), then competition should rapidly become an important factor in the survival of the species represented in areas of the bings where vegetation is well developed. There is no evidence of this successional stage developing from the data collected on the bings, although there are areas at the base of all of the sites where ground cover is complete and interactions between individual plants and species must be influencing the distribution of vegetation.

On the middle slopes of the bing the composition of seed rain will change with distance (length and height) from the local seed source, both in abundance and in composition. The overall number of seeds will decrease and the proportion of wind, and bird or animal, dispersed seeds will increase. The proportion of large seeds will decrease and only be represented by bird or animal dispersed species (Again this is hypothetical for the reasons described previously). The numbers of surviving individuals (per metre squared for example) on the middle slopes decrease with distance from the base and there is an increase in the proportion of species dispersed by wind and birds or animals, reflecting the change in composition of the seed rain. Where the sides are steep and the substrate is unstable there is a low survival rate in many species because of lack of safe sites as described by Jumponnen *et al.* (1999). Species diversity is lower than at the base of the site and vegetation is very sparse. Lack of competition and limited seed sources leads to strange combinations of plant species. On the middle slopes of unmanaged sites, patches of *Fragaria vesca* and *Leucanthemum vulgare* (wild strawberries and ox eye daisies) cover 100 m^2 patches of substrates and form a common combination on many sites although there is a distinct lack of other species (Figure 6.3). *Sedum acre* (biting stonecrop) also covers large areas but only on one bing site, Greendykes (Figure 6.3). This species is occasionally recorded in West Lothian, on dry-stone dykes and rocky outcrops (Smith *et al.*, 2002), although this colony may be a garden escape. As already noted *Reseda luteola* (weld) is common to all bing sites, frequently in association with *Senecio viscosus* (sticky groundsel) although both of these are very rare in the surrounding landscape (Smith *et al.*, 2002) (Figure 6.3). These and other similar bing vegetation 'types' have very sparsely distributed, or no, grass species associated with them. Continuing with the vegetation model on the middle slopes, there are also frequent but isolated, individual representatives of large seeded species, usually trees or shrubs, suggesting that a seed has become trapped and has germinated in a suitable microsite instead of rolling down the slope or being eaten. This appears to be the main situation when 'safe sites' are more important to the vegetation composition than seed dispersal and production. The vegetation patterns and species groupings are very dynamic, often due to physical disturbance, and are unlikely to become stable for many decades, even centuries.



Fragaria vesca and *Leucanthemum vulgare*

Sedum acre

Senecio viscosus and *Reseda luteola*

These represent some of the unusual vegetation combinations that are common to the middle slopes of the bing sites. Although they are comprised of locally rare and occasionally alien species, they are novel, natural communities.

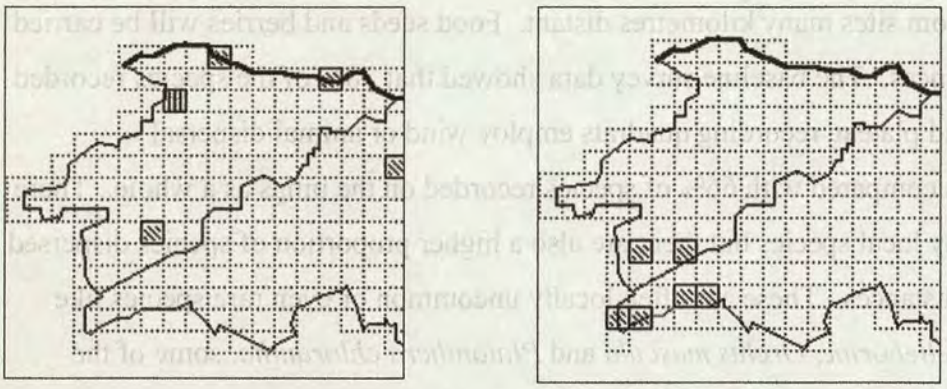
Figure 6.3 Examples of middle slope, bing vegetation types

The slopes of large, high bing sites like Greendykes, Five Sisters, Niddrie and Faucheldean, are unlikely to stabilise and the species composition of the middle sections of these bings will remain different from the vegetation at both the top and base. The middle slopes of smaller, lower bings like Mid Breich and Oakbank are likely to lose any distinctive, middle range of species as these areas become transition zones between top and base vegetation.

At the summit of the bings, on the top and plateau areas, numbers and abundance of species in the seed rain will initially be much lower than either the base or middle areas and almost wholly composed of wind and bird dispersed seeds. There will be a higher proportion of seeds from species outwith the vegetation surrounding the site represented because of this. Some species with particularly light seeds or spores will

be carried from sites many kilometres distant. Food seeds and berries will be carried similar distances. The baseline survey data showed that 78% of the species recorded in the top and plateau recording quadrats employ wind or animal dispersal mechanisms compared with 66% of species recorded on the bings as a whole. There are still many local species but there are also a higher proportion of species dispersed from great distances. These are often locally uncommon or even rare species like *Epipactus helleborine, Orchis mascula* and *Platanthera chlorantha*, some of the orchid species that have been recorded on Faucheldean (Muscott, 1989). The proportion and, in some species, number of surviving individuals is high compared with those on the middle slopes, as survival is no longer limited by slope and the substrate is more stable. Competition is currently (2004) not a major limiting factor in the succession on the summits, but is expected to gradually play a part in stabilising the developing communities over time. The overall composition of vegetation on the tops and plateaux bears little resemblance to that at the base and middle reaches of the larger bings, or to the surrounding vegetation due to the predominance of wind and animal dispersed species.

The tops and plateaux of sites are where important refuge sites have developed for rare and endangered species of the region, both plant and animal. The plant communities include many locally rare species that are better suited to the different physical and chemical properties of the substrate on the bings and also invaders from other regions with similar substrates, like coastal dunes. Examples of these are *Anthyllis vulneraria,* first recorded in West Lothian in 1999 when it was found on Mid Breich bing. The nearest recorded seed sources are sand dunes at least 20 km away (Figure 6.4a). This species is rare throughout Scotland (Smith *et al.*, 2002; Preston *et al.*, 2002). *Lycopodium clavatum* is not so rare (Figure 6.4b) but had not been recorded in Central Scotland since before 1930 until it was discovered growing on several bing sites in the early 1970's (Smith *et al.*, 2002).



a] *Anthyllus vulneraria* b] *Lycopodium clavatum*

Figure 6.4 Distribution maps of *Anthyllus vulneraria* and *Lycopodium clavatum*
Adapted from Smith et al., 2002.

6.1.3 Seeds

The production and dispersal of seed are the main processes driving this model of primary succession on the bings. Seed rain from vegetation surrounding the site determines the species range and abundance of the initial colonisation. This, when combined with secondary seed production from established plants and long range seed dispersal from similar ecosystems, adds to the diversity of species within and between the 19 bings. Seeds from all of the sources contribute to the seed bank and can be retained for many years. The trials and measurements described in Chapter Five demonstrated the extent that mechanisms of seed ecology vary both within and between species and also that some of the variation is influenced by physical and chemical variables. Seed dynamics, however, are only one aspect of the succession and to truly reflect the process the model must include the effects of morphology and nutrient availability on the competitiveness and continued success of individual species

6.1.4 Physiological variation within species

Once established, individual species can have greater seed input to patches within the site than species from nearby communities (*Reseda luteola* and *Senecio viscosus*). Perennial species, like *Leucanthemum vulgare,* spread vegetatively from an initial colonisation to gradually occupy more space, giving them a selective advantage over

incoming species. Conversely, as the vegetation contributes to soil amelioration, some species that have remained dormant in the seed bank and previously unsuccessful species that are present in seed rain, will take advantage of the changes in available resources. Gradually, dominant species will become noticeable but due to the stochastic nature of the invasion processes these will not be the same species on all sites.

Vegetation types that are dependent on the suitability of the site for the initial invading species develop. Competition, both inter- and intra specific, slowly becomes an increasingly important factor in the development of plant communities. As demonstrated in Chapter Three, these species assemblages rarely resemble any existing or standard community-type: National Vegetation Classification for example (Rodwell, 1991a; 1991b; 1992; 1995; 2000).

The inherent plasticity of nine species was demonstrated in Chapter Five (*Trifolium campestre*, *Medicago lupulina*, *Leucanthemum vulgare*, *Tripleurospermum inodorum*, *Holcus lanatus*, *Plantago lanceolata*, *Centaurea nigra*). The causes of the variability in the physical properties of the species that were measured (plant height, flower-head and seed production, fecundity) were not always clarified but the amount of the variance that was explained by variation in the physical and chemical environment was described (Chapter Five). Morphological differences and reproductive success within these species plays a large role in their distribution and the resulting vegetation patterns. When habitat factors are less favourable the patterns caused by morphology in individual species changes. On shale bings for example, extreme physical demands can be made on shallow-rooting species and seedlings by the rapid drying out of the soil/substrate, even when there is considerable rooting depth.

6.1.5 Reactions and interactions

The physical effects of wind, rain and changes in temperature influence soil structure and, to a lesser extent, the nutrient content in the substrate. These abiotic reactions and the interactions between them are important to the bing succession as weathering has a more rapid and direct effect on the substrate structure than vegetation in the

early stages. Large laminar fragments in the top few centimetres of the bings are rapidly split into layers by a combination of freezing and thawing in winter and drying and wetting in the summer. Once separated the thin layers quickly crumble to become a more suitable growth medium for invading species. Any high concentrations of salts retained from the oil extraction processes are rapidly leached from the bing surface by rain (Chapter Three).

The colonising vegetation modifies the microclimate by shading and transpiration, and the influence of some species is intensified by allelopathy, the ability to produce toxins that inhibit the growth of other species, and sometimes their own seedlings, in the immediate vicinity. Allelopathic interactions are known to occur in several of the species that have been recorded on the bings. *Plantago lanceolata,* one of the nine species studied in Chapter Five, was demonstrated to interact, both positively and negatively, with many other species by Sagar and Harper (1961). Myster and Pickett (1992) presented evidence of strong allelopathic interference by grass species on a range of other vascular plants, for example a negative effect of *Dactylis glomerata* on *Rumex acetosella*. They also demonstrated the negative allelopathic effect of *Poa pratensis* on *Plantago lanceolata* and of *Trifolium pratense* on *P. pratensis*, and the positive effect of *Plantago lanceolata* on *Achillea millefolium* in a series of pairwise experiments. The effect of allelopathy was not measured in relation to the bing succession in this study but will have increased influence on species composition as vegetation cover intensifies and there is more competition for space.

The bing succession is highly complex. The initial invasions and aggregations of species have developed into a mosaic of patterns of vegetation over a range of spatial scales. The combined hierarchical and modular structure of the bing succession has described a model of bing succession (Figure 6.1 and 6.2) that can be evaluated with published successional models. The described mechanisms and processes of the vegetation dynamics of the succession on the bings can be compared with descriptions of other successional communities from literature.

6.2 Succession Models in Literature

Regular, short-term changes in vegetation were recognised and utilised by human, hunter-gatherer ancestors, and determine behaviour patterns in animals. Farmers have exploited seasonal variation in vegetation in the production of crops and management of animals for thousands of years. Around 300 BC Theophrastus produced the first written record of the spatial and temporal variations in the vegetation of river floodplains (Wali, 1999). The first scientific writing on succession is attributed to William King (1685) in a paper presented to the Philosophical Transactions of the Royal Society, London. This is a description of the long-term orderly patterns of vegetation change in an Irish bog. Modern authors have decried this work as representing "common knowledge" (Golley, 1977) but this is an unjust criticism considering the level of much of the scientific research that was being published at the time[1].

Models of primary succession are not a new concept in natural sciences. Erasmus Darwin (the grandfather of Charles) introduced an outline model in the notes accompanying a set of rhyming couplets on Lichen in his book 'The Botanic Garden' (Introductory quote to this chapter. Darwin, 1879) which, despite its brevity, describes the stages of succession from denuded substrate to climax vegetation.

6.2.1 Descriptive models

Present day models of primary succession began in the early twentieth century with the pioneering work of Clements. Although the earliest stages of colonisation were recognised before this time, they were of no practical use to humans and so were not considered worthy of research. The first models of succession were mainly descriptive. As outlined in Chapter 1, Clements (1916) described a conventional view of the successional process in six sub-processes (seral stages).

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[1] For example, an article 'proving from experiments' that larger wheels move more easily over obstacles (A member of the Philosophical Society, 1685), and another describing the difference between freshwater and seawater ice (Lister, 1685), appeared in the same volume of The Philosophical Transactions of the Royal Society of London as the article by King.

1. Denudation – the creation of a new environment.
2. Migration (immigration in a primary succession) – the arrival of spores and seeds.
3. Ecesis – the germination of seeds and establishment of the seedlings.
4. Competition - the contention between and within species for resources: for example nutrients and space.
5. Reaction – the modification of the environment by the vegetation from processes like transpiration, shading and mortality of individuals.
6. Stabilisation – the eventual development of a climax vegetation.

I use Clements' (1916) model as the main example because it is the most frequently referred to, either in whole or in part, by other authors when describing succession. "At the simplest level, the mechanisms outlined by Clements in 1916 remain valid today" (Wali, M, 1999). The model is wholly deterministic and each of the sub-processes leads forward to the next, finally culminating in a self-maintaining and stable, climax type of vegetation. When the bing model of succession is compared with Clements' model the first three sub-processes are comparable and each leads progressively on to the next, however, they are also happening concurrently, in different parts of the bing sites and seemingly all of the time.

New successional seres originate when an initiating process produces a bare area that is capable of ecesis and has physical factors that are essentially different from the surrounding area (Clements, 1916 - Chapter III). This describes the bing substrate immediately after dumping but also after any major disturbance event such as erosion. The sterile, bare area is first colonised by the process of migration/ immigration, the movement of propagules from the parent area into the new habitat. The position of the bare area and the communities of the surrounding landscape are both briefly considered by Clements. In the bing model distance from seed source, particularly altitudinal, is shown to influence both the rate of invasion from the surrounding landscape but also, more significantly, the dispersal agencies of species that successfully colonise the tops and plateaux. These are predominantly animal or wind dispersed species in comparison with the species for the bings as a whole (Section 6.1.2). Clements gives an example of the ease with which forested areas

can be temporarily invaded by alpine species from nearby high ground and stresses the difficulty of species invading up a slope, suggesting that only man, animals and the wind can overcome this effect that supports the observations made in the description of bing succession.

Once the initial invaders have become established, the colonies develop by the process of association. The interaction of these two processes, establishment and association, originates each successional stage by introducting new species and establishing them as characteristic or locally dominant components of the vegetation. The study of bing vegetation did not reveal dominant species but there was evidence of species characteristic of particular conditions within the bing sites, as discussed in Chapter Four. The results of the field measurements in this study showed that the mechanisms of seed production and dispersal are very strong influences on the processes of invasion and species association, a finding that is supported by Clements (1916 - Chapter IV).

"Ecesis is the adjustment of the plant to a new home" (Clements, 1916). In the field measurements and greenhouse trials on the germination success and establishment of species associated with the shale bing succession the processes of ecesis, variability in plant height, flower-head and seed production and fecundity, were demonstrated to have different influences on the success of individual species (Chapter Five). The high loss of seedlings was also discussed in the previous chapter, both the loss to predators and to desiccation. Clements describes the processes of ecesis in great detail and corroborates the findings of this study: stressing the importance of habitat on germination success, how seed dormancy can overcome temporarily unfavourable conditions and the massive loss of seeds to predation.

Sub-processes four and five are less distinctly separate in the bing model than described by Clements. Interactions between species and their reactions to the environment on the bings are a series of complex processes that are happening concurrently with stages two and three of the succession model. Indeed in the bing model, as with many primary successions, there is a frequent denudation of large areas due to the physical instability of their steep slopes. Clements suggests that well

adapted species that form mats or rosettes and have long tap-roots will ultimately stabilise the substrate on these habitats and allow a continuation of succession through to climax (Clements, 1916 - Chapter V). Such species are frequently recorded on the bings and are often abundant and the description fits the unusual association of *Leucanthemum vulgare* and *Fragaria vesca* described in Section 6.1.2. Although Clements later appears to contradict his earlier statement by declaring that the significance of the stabilisation mechanism is only revealed when the cover is destroyed.

In a primary succession each pioneer exerts some reaction in or on the substrate, through removal of nutrients and water or by shading for example. Clements argues from this that the reactions caused by pioneer species alter the microenvironment until habitat becomes unfavourable to themselves, or becomes more favourable to later invading species. It is difficult to accept that this would make evolutionary sense for species in any habitat, including the bings, as it must ultimately lead to their extinction. The inherent plasticity of many early successional species is a trait that has possibly evolved to prevent their demise under such circumstances.

The final stage in Clements' succession model is stabilisation, the eventual development of climax vegetation. The environmental changes that are caused by reaction and interaction between species in earlier sub-processes become "more favourable to the occupants than the invaders and the existing community becomes permanent constituting a climax." (Clements, 1916). The data collected in this thesis suggests that the bing succession is either still developing towards climax vegetation or that the final stage of Clements' model can not be achieved in all successions. However stability is a relative term that is scale dependant, both spatially and temporally.

Bings are far short of achieving Clements' idea of climax, but there is considerable difference of opinion in the literature on the final outcome(s) of the vegetation development in succession and also on the sub-processes within the successional processes (Gleason, 1927; Bradshaw *et al.*, 1975; Austin, 1977; Gray *et al.*, 1987; Glenn-Lewin, *et al.*, 1992; Eriksson and Eriksson, 1998; and many others). Connell

and Slayter (1977) proposed three alternative succession models based on the ability of species to modify the environment.

The facilitation model describes a succession where only certain species are able to establish on a new site and these early invaders then modify the environment making it better suited to other species. The succession continues on a forward progression towards stabilisation. This describes the succession found in the middle of the bings where species that are particularly suited to the habitat have established. The vegetation on these slopes may "progress" if the substrate becomes more physically stable as a result of this initial colonisation and this could lead to increased invasion from more competitive species that are established on the already stable lower slopes.

The tolerance model describes a succession where any species that survives can establish. The sequence of species is determined solely by their life-history characteristics and implication is that newly invading individuals of one species, if they survive and establish, will always be more tolerant of the modified environment than those species already present. Ultimately only one species will remain which cannot be invaded unless individuals die or are killed, resulting in a stable, climax vegetation. The first part of this model describes the findings of Chapter Three in this study. There was a clear link between species with the same life history characteristics within the bing habitats. However there was no evidence to suggest that more tolerant (competitive) species or groups were excluding others.

The inhibition model describes a succession where the initial colonising species inhibit the invasion of subsequent species by securing all of the available space or resources. New individuals are only able to invade on the death of the original species and may be either the same species or a new species. This model will also eventually lead to stable, climax vegetation, as short-lived species are replaced more often than long-lived species. This model does not represent any described sequence of events within the bing succession. There is no evidence of initial colonising species holding a site and preventing invasion by other species except in very small areas.

These three models appear to be variations within Clements' 1916 model in that each apply a particular set of rules to the interaction, reaction stage of succession. Each of these will be valid in particular circumstances and seem to occur in parallel in the overall bing succession. However they all suggest forward progression of succession to an ultimate stability of vegetation, a climax that is not evident even in the oldest bing, Mid Breich, which has been unmanaged since cessation of dumping in 1915.

Lawton (1987) adds a fourth model, the random colonisation model. Succession involves chance survival of different initial invading species and subsequent random colonisation by new species. Species then grow and mature at different rates. There is no facilitation and interspecific interaction is not important. This model also seems to describe some of the succession of the bing vegetation, particularly the initial random invasion and morphological variation found between and within species. The model does not, however, make provision for the consequent development of recognisable and recurring patterns within succession or the concept of assemblage of species, when established individuals of annual species, for example, have a greater input into local seed rain resulting in extension of the patch dominated, or individuals of perennial species will extend their group vegetatively.

6.2.2 Numerical models

Numerical techniques are used extensively in descriptive ecology to simplify multivariate data, to assist in hypothesis generation and to define the limits of extrapolation for results of experiments on a particular vegetation type (Austin, 1972). In this thesis, gradients, correlations and multivariate analyses were used with varying degrees of success to study the structural variations of vegetation and relate these to measured environmental factors. By these methods almost 50% of the variation in species distribution within and between bings was explained. When analysing abundance data using multivariate analysis, CCA as in this study, the percentages are expected to be at these levels (ter Braak and Šmilauer, 2002) and ordination that explains even lower percentages "may be quite informative". The remaining variation could be attributed to a wide range of factors, some of which were discussed in earlier chapters and others which may not have been considered.

Early approaches to investigate non-randomness in vegetation patterns were based on the assumption that the main causal factor was vegetative propagation (Kershaw, 1963). Statistical evidence of non-randomness (as produced by Monte Carlo Analysis) was used in this thesis solely to demonstrate that particular small groups of species appeared together more frequently than expected by chance. As pointed out by Kershaw (1963) demonstration of the existence of non-randomness does not assist the understanding of the underlying mechanisms and processes causing non-random distribution. Numerical models can be used to provide empirical measurements within the structure of a subjective descriptive successional model. Difficulties arise with these analytical techniques because they are based on a mathematical model of linear correlation between sets of vegetation and environmental variables.

Multivariate correspondence analyses overcome the problems of violation of the assumption of linear response by adopting a unimodal response curve (ter Braak and Prentice, 1988). However despite their mathematical complexity the analyses can only be used to support existing or generate new hypotheses, they cannot use data to describe succession unless the data include a known time-line or chronosequence. In Chapter Four, Detrended Correspondence Analysis (DCA) and Canonical Correspondence Analysis (CCA) confirmed many of the vegetation patterns that had been detected using more simple mathematical tools and demonstrated the extent that environmental components were the correlated with the variation. The analyses also drew attention to species groupings that had not previously been evident. A mathematical assumption that can be problematic within correspondence analyses is that environmental factors are included as independent variables, and there is no consideration of detrimental, beneficial or otherwise proactive relationships between them.

6.2.3 Experimental models

The experimental approach to discovering the mechanisms and processes of succession is sometimes no more effective than the mathematical descriptive approach. The consequence of variation in each mechanism and process could be measured on every species in every community in every sub-process of the

succession. This is clearly impractical. However in experimental models the effects of many components of succession, competition for example, are often gauged on the measured reaction between only two species under artificial conditions. This is true of experimentation throughout the twentieth century from Gause's (1934) classical work on two species of laboratory Paramecium to more recent work on plant competition (Damgaard, 1998). Gibson *et al.* (1999) also suggest that simple pair-wise species mixtures can be used to assess the effects of different treatments on competition and propose that "unless plant interactions can be demonstrated under green-house conditions they are unlikely to be of importance". Designs for multiple species glass house experiments tend to suffer from lack of randomisation or lack of independence (or both). Field conditions are so complex that manipulative experiments and field trials have to be designed to run over many seasons with a large number of replications and controls. When field measurements and measurements from greenhouse trials for the same trait are compared they often bear no resemblance to each other. As discussed in Chapter Five (5.7.3) for example, glasshouse experiments have been shown to result in higher germination rates than field trials for arable weeds (Roberts & Ricketts, 1970; Graham & Hutchings, 1988), and in this study when no *Centaurea nigra* seedlings emerged from the bing seedbanks germinating under greenhouse conditions yet large numbers of plants, including seedlings were recorded in the field.

6.3 Post-industrial Sites of Primary Succession

This section will compare the mechanisms and processes of succession described in the model of the bing vegetation with man-made waste and post industrial sites where primary succession has been described in literature (Salisbury, 1953; Marrs and Bradshaw, 1993; Zhang *et al.*, 2001). Despite being described as bearing "a strong resemblance to cones of ash thrown out by modern volcanoes" and being "indeed volcanic in some respects" (Cadell, 1925) the bings are very much post industrial sites (Chapters One and Two) and, as determined in Chapter Four, the substrate of shale bings shares many physical properties with that of other types of large-scale industrial waste (china clay waste, colliery spoil, gravel pits, derelict land

and quarries). The range of post-industrial sites is as varied as the number of industries that created them.

In West Lothian there are 458 ha of designated derelict land, including 139 ha of oil-shale bings, and the total area of dereliction for Scotland is 7,741 ha (Scottish Executive, 2004). Most of the wasteland in Britain has resulted from the decline or disappearance of industries established during the Industrial Revolution and coal spoil forms some of the largest man-made waste sites in Europe.

6.3.1 Coal

There are two main methods of mining coal that each result in a different type of spoil: strip-mining and deep mining. Strip mining in the United Kingdom is small scale and current (2004) government legislation requires that restoration is closely monitored to the extent that arable crops can often be successfully grown immediately after the overburden has been replaced. This means that there is no opportunity to observe or record natural succession. In central Europe, however, large scale strip mining for lignite (brown coal) is carried out on a massive scale.

Prach *et al.* (1999) describe a succession on the mine spoil sites of North West Bohemia in the Czech Republic with steep, free-draining slopes in three stages beginning with a bare substrate and no vegetation at year one, followed by a stage with dominant perennial herbs from 2 years onward with a third stage of dominant grasses developing from fifteen years. The description of limited species assemblages and cover recorded on middle slopes in the succession model of vegetation on the bings, for example *Sedum acre* or *Fragaria/Leucanthemum* mix, corresponds to the early seral stage on steep slopes described by Prach *et al.* (1999).

In sites with no steep slopes, but still free draining, they describe a seven-stage succession (Table 6.1). Succession on these sites is rapid by comparison with that recorded on the shale bings and after thirty years there is a near complete herb layer cover dominated by *Arrhenatherum elatius*, with *Betula pendula* and *Sambucus nigra* constituting a strong woody species presence (Prach *et al.*, 1999). In contrast a stand of *B. pendula* has established naturally in one small flat area at the base of Mid

Breich bing over the last twenty years, although it is now almost 90 years since dumping ceased, and there are a few individuals of *S. nigra* established at Greendykes after 80 years. There is, however, strong evidence that the succession on the strip-mine spoil of North West Bohemia is following the sub-processes as those found on the shale bings, although the exact species compositions are not the same and the rate of succession is much more rapid in the Czech Republic.

Table 6.1 The seven stage succession of coal strip mine spoil

The seven stages of succession on flat and slightly inclined, coal strip-mine spoil sites in the Czech Republic(adapted from Prach et al., 1999). Species highlighted with an asterisk (*) are either locally rare, in West Lothian, or have never been recorded in the county (Smith et al., 2002)

description of seral stages	years from cessation of dumping	typical species	comments
initial stage or pioneer plants	1-3	*Polygonum lapathifolium** *Senecio viscosus* *Chenopodium spp.*	low total cover
initial stage or pioneer plants	4-6	*Atriplex sagittata**	dense and tall cover especially in depressions
initial stage or pioneer plants	7-8	*Carduus acanthoides** *Sisymbrium loeselii**	stage occurs and persists more on dry sites
stage with dominant perennial herbs	9-16	*Tanacetum vulgaris* *Artemesia vulgaris Cirsium arvense*	stage mixes with one or more adjacent stages
stage with dominant grasses	17 onwards	*Calamagrostis epigeios** *Arrhenatherum elatius* *Agropyron repens*	succession is arrested after about 30 years in stage of grasses mixed with scattered shrubs and trees
stage with shrubs	17 onwards	*Sambucus nigra* *Rubus spp.*	stage mixes with one or more adjacent stages
stage with trees	17 onwards	*Betula pendula* *Acer pseudoplatanus* *Fraxinus excelsior*	stage mixes with one or more adjacent stages

Richardson (1975) indicates that in coal spoil from deep-mined coal extraction the physical properties of the substrate control plant growth and the rate of succession, particularly particle size and water holding capacity. Immediately after tipping the coal spoil is free draining, like oil shale spoil, but weathering rapidly reduces permeability so that the surface becomes waterlogged in wet weather and in dry conditions a crust forms that does not allow seedling penetration. The greatest

difference between the substrate of coal spoil heaps and the bings, however, is pH. The oil-shale spoil is neutral to basic on all bing sites, even after more than ninety years, however acidity develops extremely rapidly on most coal spoil heaps (Gemmel, 1977) although Hall (1957) recorded tips that were still neutral after 40 years. These differences in the chemical properties oil-shale and coal spoil do not affect the successional process but influence the species composition of the communities that develop. The literature describes two main vegetation outcomes of succession on coal spoil (Table 6.2), the first leads to woody communities (Hall, 1957; Titlyanova and Mironychevka-Tokareva, 1990) and the other arrests as grass- or heath-land (Hall, 1957; Weigleb and Felinks, 2001). The successions follow the same initial stages but demonstrate the variability of time scale that can occur between the sub-processes in different geographical regions, although this is less extreme in the woodland sites.

Table 6.2 Examples of temporal variation in successional stages of coal spoil

The two main vegetation outcomes on coal spoil described in the text; one succession results in woodland and the other succession arrests as a grass/heathland. Adapted from Hall, 1957; Titlyanova and Mironychevka-Tokareva, 1990; Weigleb and Felinks, 2001.

reference	pioneer	forb/ grass	grass/ scrub	climax (*sic*)	vegetation type	region
Hall, 1957	10-15	15-80	60+ →		grass/heath	NE. England
Titlyanova & Mironychevka-Tokareva, 1990	4-15	15-40	30+ →		meadow steppe	Siberia
Hall, 1957	4-10	10-30	30-100	80+	oak woodland	SW. England
Weigleb & Felinks, 2001	4-10	10-20	20→	100+	woodland	Lusatia, Germany

On the oil-shale bings there is evidence of different successional stages occurring simultaneously within sites and some sites retain pioneer vegetation after more than 90 years, suggesting that the temporal discrepancy in sub-processes is being driven by variation in the environment.

6.3.2 China clay (Kaolin)

The waste material from the production of china clay (kaolin) is mostly deposited as rolling hills of quartz crystals (sand) interspersed with mica lagoons and occasional dumps of overburden, although these are usually covered with sand (Bradshaw *et al.*, 1975). Much of the research in Britain has been carried out on the sand deposits, by the Department of Botany in the University of Liverpool (Bradshaw *et al.*, 1975; Marrs *et al.*, 1980a; Roberts *et al.*, 1980; Marrs and Bradshaw, 1980; Marrs *et al.*, 1980b; Roberts *et al.*, 1981; Marrs *et al.*, 1981). This series of papers describes ecosystem development in relation to nutrient availability in the substrate. There is also some literature from the University of Georgia in the United States of America on the restoration of overburden (May, 1975; Haddock, 1997).

The quartz sand deposits studied by the Liverpool group are large mounds of open free-draining material in an area of high rainfall so that surface desiccation occurs only in summer making them physically similar to shale bings. The chemistry of the substrate is also similar to the bings, the main exception being the significantly lower levels of calcium, which are reflected in the lower measures of pH (Table 6.3).

Table 6.3 Comparison of the substrate chemistry in China clay waste and oil-shale spoil

The results of nutrient analysis of substrate at two china clay spoil heaps, Maggie Pie and Lee Moor (adapted from Bradshaw et al., *1977), and two shale bings, Mid Breich and Greendykes (from this study). The mean measure of K, Mg, Ca, P and N in parts per million and the pH are recorded for each site. All four sites are unmanaged. * Nitrogen values were not available for the two unmanaged bing sites but measurements at two managed bings were less than 2 parts per million.*

site	substrate	K	Mg	Ca	P	N	pH
Maggie Pie	china clay	10	16	85	2.0	9	4.5
Lee Moor	china clay	8	14	90	4.6	11	4.5
Mid Breich	oil-shale	11	17	300	1.9	*	6.6
Greendykes	oil-shale	21	51	398	5.1	*	6.5

The lower pH in the china clay waste also results in colonisation by a different group of vascular plant species. There is a slow invasion by calcifuge grasses and shrubs, a strong legume presence and *Salix caprea* and *Rhododendron ponticum* survive well in the later stages of succession. Bradshaw *et al.* (1977) suggest that the climax

vegetation will be acid oakwood. While this is similar to the findings on some coal spoil sites (Table 6.2) it is not comparable with the recorded vegetation on shale bings.

Roberts *et al.* (1981) outlined successional stages in natural colonisation of china clay waste in their description of vegetation changes on a group of sand tips ranging in age from 16-116 years. Most of the species recorded on the china clay waste are common native species and many of them also appear on the species list for the shale bings (Appendix 6). There are no annuals included in the vegetation descriptions, however, and eight species are recorded at more than 10% cover, all trees or shrubs. On the bing sites annuals were recorded in most areas and only two species, the grasses *Holcus lanatus* and *Deschampsia flexuosa*, were recorded at more than 10% cover. A low species diversity was recorded in the china clay waste study with the maximum number of species in any quadrat being 13, compared with 28 on the shale bings (the mean number of species over 340 bing quadrats was 13), and the china clay sites seem more homogeneous.

Recent studies, in the south eastern United States, to establish the soil conditions that encourage pine growth on kaolin spoil, compared stands of high productivity with those of low productivity (Haddock, 1997). Nutrient and physical properties of the spoil were measured but none of the measurements indicated significant or consistent differences in the soils where faster tree growth occurred. Similar inconsistent information was encountered in this study of the shale bings when trying to relate variation in the chemical and physical properties of the substrate to morphological variance in individual plant species (Chapter Five).

6.3.3 Quarries

Man-made primary sites resulting from non-ferrous ore extraction, sand and gravel workings, and stone and slate quarries are usually on a smaller scale than the massive waste from industry. In the past, most of the quarry and small-scale mining sites were abandoned to natural restoration, mainly because they were situated in rural areas. The scale of wasteland from quarrying has increased in recent years, however, with super-quarries being planned in very fragile ecosystems, including the Peak

District National Park (Bradshaw and Chadwick, 1980) and restoration schemes are more prevalent. Unlike industrial man-made sites the successional time scales studied in some quarries can be measured in millennia, rather than decades, for example on the Stone Age flint mines in the chalk of Norfolk (Ranson and Doody, 1982).

Quarry substrates can be either acid or alkaline, with very low levels of plant nutrients. They also have combinations of extreme physical conditions; steep and flat surfaces, coarse and fine particles, stable and mobile spoil, and extremes of wetness and dryness; making them very similar in structure to shale bings. Most of the literature describes the vegetation of chalk, limestone and other carboniferous quarries (Davis, 1982; Bradshaw and Chadwick, 1980; Hepburn, 1955) but there is reference to the invasion of slate quarries, which have a hard acid substrate, by Bradshaw and Chadwick (1980). Many common species are recorded on quarry sites and on the quarry floors a varied but very evenly distributed flora develops (Davis, 1982). Descriptions of present vegetation and lists of common species are similar for alkaline quarry sites throughout the United Kingdom although there is considerable variation in the less common species both within and between sites (Hodgson, Davis, Ranson and Doody, Gray, Finegan and Harvey, all in Davis 1982; Hepburn 1955).

Regardless of the species composition of the vegetation, however, the mechanics and processes of succession follow those described in the descriptive models of bing succession summarised earlier in this chapter (Figures 6.1 and 6.2). The establishment of any species is a chance occurrence that depends on dispersability of propagules and tolerance of individuals to the biotic and abiotic conditions (Gray, 1982). The considerable diversity in the composition of vegetation within and between quarries is dependent on such factors as the time since abandonment and the heterogeneity of the physical and chemical environment (Finegan and Harvey, 1982). These are similar to the statements that have been made in this thesis regarding the variations in bing vegetation.

6.3.4 Other man-made sites

Other man-made habitats that are potential sites of primary succession include arable land, motorway verges, ski-slopes, derelict inner city sites, railway embankments and canal banks. The vegetation on many of these anthropogenic sites has been studied, usually with a view to restoration or reclamation to some degree of naturalness. With the exception of arable land, the physical properties of the sites are similar to those found on shale bings. The sites often have steep slopes with large particles, making them unstable, and are usually free-draining. Construction materials are often brought in from other parts of the country so the chemical composition and pH of the substrate are likely to be different from the surrounding landscape. Tsuyuzaki (2002) summarises the properties of the substrate on a skislope in Japan as "low in nutrients and the seedbank is absent" because of the erosion of all surface soil. This would make it a highly comparable site with bings and other industrial sites.

6.4 Natural Sites of Primary Succession

Many of the physical and chemical properties of man-made primary sites are also shared with natural primary sites (volcanoes, glaciers, scree, shingle and sand dunes). This section will continue the comparison of the model of bing vegetation described in this chapter (Section 6.2) with the processes of colonisation and succession described in literature from studies of islands (MacArthur and Wilson, 1967; Cronk, 1989; Schmidt and Schmincke, 2002), volcanoes (Ernst, 1908; del Moral, 1993; Lawrence and Ripple, 2000) and sand dunes (Cowles, 1899b; Lichter, 2000).

6.4.1 Islands

As described in Chapter 1 the oil-shale bings can be compared to islands. Their steep slopes and height, compared to the surrounding low-lying landscape, combined with the unique physical and chemical characteristics of the shale substrate, effectively isolates each bing from the surrounding area. The bings constitute islands of a different environment, in a sea of agricultural land. The individual area and height of these islands should be a determinant in regulating the occurrence and abundance of plant species (Wardle *et al.*, 1997) and the colonisation by plants

should therefore follow the succession and vegetation patterns found on natural islands. The literature on island vegetation and successions is extensive and includes both general (Cronk, 1989; Schmidt and Schmincke, 2002) and very specific information (Holt, 1992; Smith and Steenkamp, 2001). A strategy of colonisation on islands is presented as a series of theoretical equations, structured around r and K, by MacArthur and Wilson (1967) and describes the processes whereby species richness per unit area should increase with island size. These are based on an assumption of both birth and death being density dependent. Holt (1992) elaborates on this model, pointing out that colonisation does not take place consistently over the whole island and that spatial structure and dynamics of populations within islands can both enhance the overall colonisation rate and reduce extinction rates. The model based on data from the bings would appear to support Holt's suggestion of independently dynamic patches of vegetation within a site.

However the island biogeography theory (MacArthur and Wilson, 1967) also assumes that the surrounding matrix (the sea) is totally incompatible with the island and so does not contain species or processes that can influence the island landscape. In a landscape context, the bings are islands in a sea of agricultural land, the matrix is not incompatible with the island and there is considerable recruitment of species from the surrounding area (Cook *et al.*, 2002). This process was demonstrated by the invasion of immediately local species to the basal slopes of the bings, described in the model in Section 6.1.1, as was the relationship between the extent of this invasion and the size, or more importantly the height, of the site. The seed dispersal powers of most flowering plants are limited (Miles and Walton, 1993) and islands, including oil-shale bings and other islands of industrial waste, are often isolated from similar habitats. In the bing model, colonisation is dependent on the availability of suitable seed sources, in terms of habitat requirements, that occur in close proximity: a model that is supported by del Moral (1993) in his description of the succession on Mount St. Helens. Initially this leads to a species poor flora, as found on the steep middle slopes of the larger bings, that reflects the stochastic order of species arrival by dispersal and is supported by theory developed independently in the early 20th century by Gleason (1926), Lenoble (1926) and Ramensky (1926) as an alternative to

the deterministic succession model presented by Clements (1916). As the succession continues larger bings (or islands) and those near suitable propagule sources should have greater species richness than sites that are smaller and more distant (Holt *et al.*, 1995).

6.4.2 Volcanoes

Volcanoes are effectively another type of island, indeed many oceanic islands are formed as the result of volcanic activity. The physical similarities between volcanoes and bings were pointed out by Cadell (1925) and have already been remarked on earlier in this chapter. The colonisation of volcanoes and volcanic islands has been the source of major long-term analyses of primary succession for more than a century (Ernst, 1908; van Borssum Waalkes, 1960; Bush *et al.*, 1983; Whittaker *et al.*, 1989; Partomihardjo *et al.*, 1992 [Krakatau group]. Wood and del Moral, 1987 and 1988; Dale, 1989; del Moral, 1993; Lawrence and Ripple, 2000; del Moral and Jones, 2002 [Mount St. Helens]).

All life on the Krakatau island group was extinguished in August 1883 when the three islands, Pulau Rakáta, Pulau Sertung and Pulau Rakáta Ketjil[2], were covered with up to 30 metres depth of ash and pumice when the supposedly extinct volcano, Krakatau, erupted (Ernst, 1908). Continuing volcanic activity over the next 50 years resulted in the emergence of the new island, Anak Krakatau, in 1930 (van Borssum Waalkes, 1960). The vegetation has been studied and recorded on both the original islands, since the 1883 eruption, and on Anak Krakatau, since its emergence. The vegetation of Mount St. Helens in Washington, USA was similarly devastated from a single eruption in 1980 (del Moral, 1983) but only towards the north, the vegetation on the southern flank of the volcano was not destroyed. The two sites had very

[2] Sertung is also referred to as Danan and Rakáta Ketjil as Panjang or Perboewatan in some texts and the Anglo/Dutch names of Krakatau (locally this is the name of only the volcano), Verlaten Eiland and Lang Eiland are also used. There are also various spellings of the Indonesian names for the three islands.

different vegetation prior to the volcanic activity that reflected their geographical location.

The Krakatau group is surrounded by the Selat Sunda, a strait between the Java Sea to the north and the Indian Ocean to the south, and is situated in a region of species rich tropical forest islands in Indonesia (Whittaker *et al.*, 1989). Mount St Helens is a terrestrial volcano located in the Cascade Mountains on the west coast of the USA in a temperate region, with species poor sub-Alpine vegetation (USGS, 2003). The nearest seed sources were in close proximity to the new substrate due to the incomplete destruction of vegetation on the volcano but, despite this, invasion was slow and after six years colonising species were very sparsely distributed (Wood and del Moral, 1987). The invasion and succession of the Krakatua Group after the earlier volcanic activity was very rapid, despite the nearest seed sources being islands 19 - 27 Km away that were also damaged by the eruption, and mainland Java and Sumatra, 35-45 Km distant (Table 6.5).

Table 6.4 The vegetation recorded on the Krakatau Group

The number of species, and their dispersal mechanisms, recorded on the three islands of the Krakatau Group in 1886, 1896 and 1979-83; and on Pulau Sertung in 1897, 1906 and 1979-83 (adapted from Ernst 1908 and Whittaker et al., *1989).*

site	Years from eruption	no. of spp	notes
Krakatau group	3	28	11 cryptogams- only 2 belong to local islands 17 phanerogams - 11 sea dispersed, 6 wind dispersed (4 composites and 2 grasses) + 7 species represented only by seeds
Krakatua group	13	65	12 cryptogams 53 phanerogams - 32 sea dispersed, 17 wind dispersed, 4 animal dispersed + 26 species represented only by seeds
Krakatau group	96-100	76	17 cryptogams and 59 phanerogams - 42 sea dispersed, 13 wind dispersed, 21 animal dispersed
Pulau Sertung	14	15	cryptogams and phanerogams (numbers not given)
Pulau Sertung	23	42	recorded within 1 hour by 2 people 7 species not recorded on Pulau Rakáta
Pulau Sertung	96-100	31	6 cryptogams and 25 phanerogams The reduction in species numbers is probably due to volcanic activity in the 1950's (Whittaker *et al.*, 1989)

The early differences between the vegetation and species diversity on the islands have not levelled out in the ensuing decades, as might be expected if the succession was moving towards climax (Whittaker *et al.*, 1989). There is evidence of a high species turnover on the Krakatau group between 1896 and 1983.

Many of the earlier studies of the Krakatau group (Ernst, 1908; Van Borssum Waalkes, 1960; Bush *et al.*, 1983) concentrated on the analyses of species/area relationships rather than species/time relationships however these earlier data sets were used by Bush and Whittaker (1991) to investigate the primary colonisation of the islands. Their objective was to identify the patterns of recruitment and extinction in succession, for higher plants, birds and butterflies, from start (the eruption of 1883) to equilibrium. They concluded that the success of colonising species was habitat determined and the dispersal mechanisms and ecologies of individual species would play a major role in determining the succession. The arrival of species, or groups of species with similar ecologies, would be stochastic in both order and timing (Bush and Whittaker, 1991). The emergence of Anak Krakatau in 1930, and the repeated activity from this volcano, resulted in significant disturbance to the vegetation of P. Sertung and P. Rakáta Ketjil in 1952/52, 1960/61 and 1972/73 (Bush and Whittaker, 1991; Partomihardjo *et al.*, 1992). However a large turnover of species within the succession on the Krakatau group had already been recognised (Whittaker *et al*, 1989) and at the same time the new island provided habitats that had not been found on the other islands for several decades (Bush and Whittaker, 1991).

On Mount St Helens recovery was initiated within 1year of the eruption (Dale, 1989) with the arrival of *Chamerion angustifolium*[3]. This species and other wind dispersed species were the most common early colonisers and 34 species were recorded by 1986, 17 wind dispersed, and the remainder animal or unspecified (Wood and del Moral, 1988; Dale 1989). Nitrogen fixers and several tree species had already established by this stage, there was strong clumping of species and evidence that

[3] The earlier nomenclature of *Epilobium angustifolium* L. is given in the original text.

Lupinus species had survived the volcanic activity and that individuals were regenerating from buried rootstocks, not seed (Wood and del Moral, 1988). However by 1996 overall diversity had stabilised (del Moral and Jones, 2002; using Shannon-Weiner index of diversity H') and began to decline due to the increased cover by long-lived stress-tolerant species and the decrease in abundance of some of the pioneer species.

The overall conclusions reached in the studies of succession on Mount St. Helens are similar to those from the Krakatau group and also from the bing model. Early colonists are most likely to be wind dispersed with later colonists being better adapted to the individual habitats and longer-lived species (del Moral and Jones, 2002). The reassembly of plant species after volcanic activity is primarily stochastic, but, unlike the bings, historic events, such as the season of the eruption and the presence of any relict vegetation will play an important secondary role (del Moral *et al.*, 1995). The studies of colonisation made on Mount Usu, (Tsuyuzaki and del Moral, 1994; Tsuyuzaki, 1996) and Myake-Jima (Kamijo, et al., 2002) in Japan, and on Long Island and Motmot (Harrison *et al.*, 2001) in Papua New Guinea also support the models of succession described for the oil-shale bings. The dispersal mechanisms determining initial invasion are wind and animal (sea on island volcanoes), and species richness and composition is dependent on the availability and proximity of source propagules.

6.4.3 Sand dunes

The southern shores of Lake Michigan were the source of a series of classic studies on the plant ecology of sand dunes that was one of the first to recognise and document plant succession (Cowles, 1899a; 1899b; 1899c; 1899d). In some ways sand dunes are the closest natural site to shale bings. In common with the other primary sites, both man made and natural, that have been discussed in this chapter the dunes have a dynamic vegetation that presents opportunities to study the processes and mechanisms of plant species and how they interact with the environment (Gimingham, 1989). Like shale bings they also often have a high recreational and amenity value.

The dunes are exposed to a high light, low nutrient environment and the substrate is very free draining, like the oil-shale bings and many of the primary sites described in this chapter. The lack of shade combined with high winds leads to extremes of surface temperature and can cause desiccation of species with short roots, although this is compensated to some degree by considerable condensation of dew from rapid night cooling (Cowles, 1899a). The dunes present an extensive chronosequence of around 450 years from primary colonisation to developed ecosystem (Lichter, 2000) in a series of spatially separated vegetation types (zones).

Cowles (1899d) comments on the similarity between the dune floras of Lake Michigan and Denmark (citing Warming between 1891 and 1896). The genera and species are often the same and when they are not related they have the same life habits. More recent works on the vegetation patterns on dune formations on Lake Michigan, (Lichter 2000) and in Holland (Grootjans *et al.*, 2001) have concentrated on the constraints during succession that effect the transition from one step to the next, or that arrest vegetation development at a particular stage. The bing model of succession is again supported as both authors conclude that the rate of vegetation development and the establishment of individual species are dependent on the availability of suitable seed sources. Secondary factors can include seed predation and seed or seedling desiccation (Lichter, 2000), lack of dispersal agents (Grootjans, 2001) and episodic burial (Lichter, 2000).

6.4.4 Glaciers

Another classic series of papers on primary succession were produced by Cooper (1923a; 1923b; 1923c) using vegetation data from land gradually exposed by glacial retreat at Glacier Bay, Alaska. The investigations followed observations by John Muir in his diaries (published in 1915) on finding the remains of a forest that had been devastated during an earlier advance of the glacier (Cooper, 1923a). Three stages of succession are described by Cooper (1923b) based on "the increasing dominance of a new growth form".

1. The pioneer community: evident in areas closest to the glacier front and in patches within the other stages. Vegetation varies in density from scattered

individuals to close cover. This is synonymous with the earlier description in this chapter of vegetation on the steep middle slopes of the shale bings

2. The willow alder community: generally occupies the steep middle slopes. The thickets are larger and closer together with distance from the receding glacier front.
3. The conifer forest: in 1923 this was an almost pure stand of young *Picea sitchensis* with occasional *Tsuga* spp.

Jones and Henry (2003) described a similar directional succession on the glacier foreland of Ellesmere Island in the Canadian High Arctic. Using Twinspan and canonical correspondence analysis they identified four main stages of dominance over a 44 year chronosequence, moving from moss dominated vegetation, to graminoid-forb, to deciduous shrub-moss and culminating in evergreen-dwarf shrub-moss (Jones and Henry, 2003).

The overall conclusions from research and description of glacier foreland suggest that, in this habitat, primary succession follows the classical deterministic model of Clements (1916) as new, denuded land is revealed by the retreating glacier. This is in contrast to the bings and other primary succession habitats, both natural and man-made, where distance from suitable seed sources and regular physical disturbance of the substrate leads to delay or arrestment of vegetation development.

6.5 Discussion and Conclusions

It is doubtful if any single model can effectively represent the mechanisms and processes of succession and Clements' (1916) six sub-processes, with the possible exception of stabilisation, are a useful way of dividing the process. When succession is considered, either temporally or spatially, the vagaries within each stage that pertain to individual sites and conditions can be described and discussed in relation to the original model. Succession is not a single process and its direction, or lack of direction, is determined by a large number of interrelated causal factors. Cause and determination imply that the process is not random (Lawton, 1987). If the process is not random then the assemblage of a new community should be predictable and comply to set of rules (Odum, 1969). In a mini-review of assembly rules, using

examples from a wide range of literature on both plants and animals, Belyea and Lancaster (1999) proposed that three main factors influence the formation of communities; dispersal constraints, environmental constraints and internal dynamics. Succession is a gradual assemblage of species into communities within an environment that will ultimately evolve into an ecosystem. The main factors that influence the outcome of vegetation successions are also dispersal constraints, environmental constraints and internal dynamics. The mechanisms and processes governing succession therefore comply with assembly rules.

6.5.1 Model comparisons

The bing model presented in this chapter was based wholly on observations made in the field, analysis of vegetation data collected in the field and from simple glass house trials as described in earlier chapters. These observations provided fundamental information supplying the answers to 'which species are present on the bings?', 'how abundant are they?', 'where are they?', 'how did they get there?' and 'what vegetation patterns, if any, can be found?' thus allowing direct comparison with literature from other sources that was not previously possible.

The successional model of the bing followed the general patterns and early stages of vegetation development outlined in the broad descriptive models of succession (e.g. Watt, 1947). The patterns of vegetation recorded in the individual positions within the bings (top, middle and base) represented chronosequences pertaining to the succession and were comparable with models of the internal dynamics of seral stages described in the literature (e.g. Connell and Slayter, 1977). The bing model of succession follows the early stages of succession described by Clements (1916) and these stages are influenced internally by (at least) three, concurrent, processes that influence small-scale patterns in vegetation and make each succession unique: within species variation in physiology, seed production and the ability to establish within the new community. Pattern at low level intensity, as is found in most of the bing vegetation, is controlled by small numbers of factors and Kershaw (1963) confirms that these can usually be attributed to the morphology of individual species (Kershaw, 1963).

Sociological patterns are the product of interrelated causal factors: partly the properties of the plants, the interaction of species on species, individuals on individuals, partly reflecting the microenvironment. The patterns can be modified by the microenvironment and are dependent on the competitive ability of individual species. The age of individuals can affect competitive ability, the physical or chemical environment may be modified by one species thus affecting the distribution of another species and allelopathic interactions between species can either inhibit or enhance establishment. There was no evidence of species competition from analysis of the bing data but the consistent grouping of particular species with similar habitat requirements demonstrates strong sociological patterns (Chapter Three). Under contrasting conditions the outcome of interaction between the same two species might be different. For example *Leucanthemum vulgare* and *Fragaria vesca* form an almost exclusive association on large areas of the steep middle slopes of the bings, yet each of the species is an individual and major component of the more species-rich, grassland community of the tops and plateaux.

Microtopography causes patterning in vegetation as a result of several environmental factors. The physical and chemical character of the substrate, drainage, water availability, leaching, nutrient supply and pH, will reflect the non-uniformity of the soil surface. Extremely small changes in pH or ion concentration will result in a vegetation pattern (either directly or indirectly). Chemical analysis of samples from the bing substrate (Chapter 4) demonstrated that there was considerable variation in pH, calcium, phosphorus and potassium concentration both within and between sites and Snaydon (1962) recorded that the same nutrients can vary by a factor of three within a distance of only 0.6 m in soil sampled from sites in Hampshire and Wales.

Succession is also influenced externally. The models from literature identify the main factor determining the rate and direction on succession as the availability and suitability of invading propagules from local sources. They also agree that the large-scale physical environment, altitude, latitude, isolation and climate, can impose constraints on the invasibilty of a site. These are the same mechanisms and processes of succession described in the bing model therefore information collected from the bing sites can be used to formulate general hypotheses on succession.

6.5.2 Primary comparisons

The comparison of the bing vegetation with other primary sites, as opposed to general models of succession, introduced some interesting implications regarding the influences of rate of development and spatial pattern that may be unique to primary successions.

There is a major point of discussion regarding year zero of a primary succession. Bush and Whittaker (1991) consider that the recurring volcanic activity and associated vegetation setbacks should be part of a single successional model of the Krakatau group, but Partomihardjo *et al.* (1992) argue that the succession restarts after every major volcanic activity. On the studies of post-industrial sites year zero is usually considered to be the date of cessation of tipping unless there is documented evidence to suggest that some parts of a site have been undisturbed for longer than others. Much has been made in literature of the long-term, continuous study of primary succession on the Krakatau group. Perhaps this should be challenged and a case made for reviewing each additional disturbance as a new primary event.

A likely influence on the developing vegetation in primary successions that has not been investigated in this study is the "founder effect" that can limit the genetic variation of species arriving as early colonisers especially if a population is formed from the progeny of one, self-pollinating individual. Gray (1987) attempted to ascertain whether perennial pioneer species change genetically during succession but the results were inconclusive because of the intrinsic impossibility of untangling the temporal and spatial influences of successional environments from the inherent phenotypic variation of plants. However he does suggest that succession "is a potent force retaining plasticity for many traits in plants" that enable them to adapt to unpredictable resource levels in new habitats. I have been unable to find any published research on the influence of succession on possible genetic changes in annual pioneer species. It seems likely that the ability of some individuals to reduce their growing time, and set large amounts of seed when conditions are sub-optimal, would result in rapid selection for a particular genotype, however, a high proportion

of ruderal and pioneer species are apomictic and therefore retain the genotype of the original invading individual(s).

The proximity of seed sources to the succession site is recognised as important to the rate of recruitment and extinction on all sites. On primary sites however there is the additional constraint that the available seed has to be from species suited to the, usually, very different conditions on a new substrate. When suitable sources are a great distance from the site there can be a long period of invasion by local, short-lived, generalist species before longer-lived, better-adapted species establish. This has the effect of slowing the succession, but also increases the possibility of greater diversity within plant communities on the site in the long term. The situation is further complicated when there is a suitable seed source nearby as was exemplified in volcanic succession. The close proximity of source species to Mount St. Helens compared with the more distant sources after the initial eruption in the Krakatau group was a restraining factor in the rate of species turnover as there will always be continued immigration by the same species into the site. Wood and del Moral (1987) suggest that there should be a clear distinction made between the source pool, defined as the total species in the immediate vicinity, and the immigrant pool, which is limited to those species from the source that are actually colonising the site. On the shale bings, the lack of suitable species in the surrounding landscape has led to a diverse combination of species from various external sources forming unusual assemblages. Each site has its own unique communities because the individual bing sites stand alone, surrounded by different types of agricultural land and are continually being showered by a diverse seed rain. Conversely the massive heaps of sand produced by the china clay industry (Section 6.3.2) were species poor and the vegetation homogeneous because the sand heaps form a single continuous mass covering a vast area (Bradshaw *et al.*, 1977; Roberts *et al.*, 1981). The initial, successful colonisers are self-perpetuating and contribute almost all of the propagules in the seed rain, except around the periphery of the sites.

The physical size and shape of primary sites varies hugely. The individual height and area of each site determines the potential heterogeneity of habitats within the site and also their distance from potential seed sources. In the study of the shale bing

vegetation in this thesis it was possible to establish that the height of the bings had a strong correlation with the dispersal mechanisms of species that established. Higher and steeper areas had a larger proportion of wind and bird dispersed species than lower slopes and the surviving species were often not representative of the surrounding landscape.

The peaks of the bings range from 100 - 240 m above sea level (a.s.l.) making them comparable in height with the lower lying islands in the Krakatau group. None of the studies of this group of islands associates possible variation in vegetation between these sites with altitude, although the highest point of P. Rakáta is 735 m a.s.l. compared with less than 200 m a.s.l. on the other islands. The larger size and height of the main island has possibly resulted in a wider range of habitats for individual species and Van Borssum Waalkes (1960) notes vegetation zones in his description of P. Rakáta. He continues, however, that they are not primarily caused by altitude (and therefore temperature) but suggests that they are attributable to differences in humidity that increase with altitude. There is no consideration of the physical problems of up-hill propagule dispersal that must be prevalent, even on the lower islands, because of the steep slopes. Recent landscape-scale analysis of the vegetation cover on Mount St. Helens by Lawrence and Ripple (2000), however, established the importance of slope gradient for revegetation in primary sites that had not been recorded in any of the other field studies on volcanoes.

So far only the effects of macrotopography have been discussed; the significance of the large-scale physical factors, altitude, angle of slope and site area, on the assembly of species during primary succession. Smaller-scale patterning, over several metres, is more likely to be caused by differences in topography, drainage, soil composition, or a combination of these (Kershaw, 1963). Weigleb and Felinks (2001) suggest that "unfavourable starting conditions" could result in grass-dominated communities persisting indefinitely in coal spoil heaps, although they do not define what these conditions are. The underlying assumption of the paper is that the succession must progress to woody, climax vegetation yet no evidence for this has been recorded in studies of many other primary sites, both natural and man-made, even after a century. On the bings there is extensive grassland on the well established larger sites that

shows little sign of evolving into woodland, despite there being little or no grazing pressure that might prevent tree establishment.

Another underlying implication that occurs throughout the literature is that lack of available nutrients (particularly nitrogen), or extremes of variation in particular elements in the substrate prevent or delay successional processes. Results of artificial manipulation of nutrients in sites have shown that their availability, when matched to optimum species requirements, can accelerate the process of colonisation (Williams, 1975; Marrs et al., 1980; 1981; Palmer and Chadwick, 1985). These manipulative experiments normally also include artificial seeding or planting making it difficult to determine which factor is actually responsible for any increases in biomass productivity. The analysis of variance in nutrients from substrate samples from the shale bings in this study showed no significant correlation with either increased growth of individuals (measured as plant height) or with increased abundance of species. Similarly Haddock (1997) found no significant correlation of improved growth of tree species with improved nutrient availability under naturally occurring vegetation in china clay overburden.

Small-scale patterning can be based on plant morphology (Kershaw, 1963). Variance in abundance of individual species will depend on the overall vegetation cover in an area. The individuality of the vegetation recorded in primary succession sites has been evident throughout this chapter. The stages of succession may not always be directional, some stages will not develop, others may be arrested but the primary successions all follow the general succession models.

The most invasible plant communities are those with a large proportion of bare ground or with frequent disturbance (Crawley, 1987). Early colonisation in all primary habitats is stochastic, but dependent on the availability of suitable propagules, and is followed by a combination of vegetative spread, or internal seed production from random centres and continued external recruitment, producing small-scale pattern. Barnes and Stanbury (1951) presented evidence suggesting that there will be an overall reduction in pattern as a community stabilises following initial succession of colonisers. Grubb (1987) expects "primary succession to lead to

a type of vegetation that is relatively constant in composition" but continues "over a sufficient area and through sufficient time." Theoretically a constant association of species is climax vegetation. Increasing stability of plant communities is also linked with decreasing intensity of pattern and should ultimately result in homogeneity of vegetation and very boring landscapes. There is little evidence of homogeneity developing in many of the primary sites discussed in this chapter, despite their all following similar assembly rules, suggesting that climax vegetation is some time off.

6.5.3 Summary

The mechanisms and processes producing the developing vegetation patterns on the West Lothian shale bings recorded in this investigation have been used to formulate a model of bing succession that has been compared with successional models from literature and with the vegetation dynamics of succession in other primary sites, both natural and man-made, thus establishing bings as acceptable models of primary succession that follow previously identified stages or sub-processes. The succession patterns on shale bings follow the same trends as those recorded on other primary sites. The development of vegetation on the bings at all scales, from macro- to micro- topographical, displays strong similarities to other primary habitats and is analogous to the development of island vegetation, particularly those communities found on volcanoes and oceanic islands. This leads me to conclude that observations of vegetation patterns and species data collected from oil-shale bings can be effectively used to predict the mechanisms and processes of succession on other primary sites.

CHAPTER SEVEN

"Many sites left to colonize naturally are of considerable ecological value."

A.D. Bradshaw, Presidential address to the British Ecological Society, December 1982.

7 General Discussion and Conclusions

The primary aim of this thesis was to address its title, "The Mechanisms and Processes of Vegetation Dynamics on Oil-shale Spoil Bings in West Lothian, Scotland". In Chapter One a series of questions were raised relating to the bing vegetation and to models of successional mechanisms and processes, Chapter Two placed the study sites into geographical, historical and geological context and Chapters Three to Six addressed the questions posed in the first chapter.

Chapter Seven will summarise the ecological value of the information gathered from this study of the vegetation of oil shale bings of West Lothian. The findings of the study will then be presented in relation to current research in restoration ecology. Sufficient data have also been generated to propose management regimes that will maintain the unique contribution of the bings to the biodiversity of central Scotland and West Lothian in particular. The main aims, as with the earlier chapters, are to address the series of questions posed in Chapter One.

What is the ecological value of the study of colonisation on shale-bings?

Can indicator species be used to identify the physical and chemical structure of the substrate?

How important are transient and transitory species to the establishment of plant communities?

Are the examples of both assisted and natural colonisation processes on bings relevant to the restoration and management of other spoil sites?

What contribution do spoil sites make to local biodiversity?

7.1 The Ecological Value of the Study of Shale Bings in West Lothian

The West Lothian oil-shale bings are unique examples of post-industrial waste sites that provide an opportunity to study colonisation on a primary succession habitat. The study of colonisation on waste ground provides interesting and instructive insight into the succession of plant communities. These are not necessarily communities belonging to recognised vegetation types: Tansley (1911) described industrial waste land as "a battle-ground for aliens and casuals" and a Universal Classification of Plant Communities[1] reviewed in the first issue of Journal of Ecology (Tansley, 1913) discounts any plant communities where there have been "displacements of natural vegetation" by man thereby excluding communities of waste sites.

The assemblages of species recorded in this study on the bings did not often comply with recognised British plant community descriptions, for example Rodwell (1991a; 1991b; 1992; 1995; 2000), but certainly formed recognisable and recurring patterns both within and between sites (Chapter Three) emphasising that waste sites are potential habitats for novel vegetation types that should not necessarily be forced into existing categories.

The groups of species recorded on the bings did not seem to follow the accepted rules of assemblage in relation to the environment either. References from literature continually stress the importance of availability of nutrients, particularly nitrogen, to the successful establishment of vegetation in a succession as discussed in Chapter Four. The range of soil nutrients, both high and low, and the exceptionally low levels of available nitrogen measured in the substrate of all sites did not seem to deter successful invasion and production of biomass and there was no evidence of any association between chemical gradients and species abundance. Professor Peter Grubb (now retired from the Department of Plant Sciences at Cambridge University) is recorded as having questioned the generality of the view that the rate of vegetation

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[1] Brockmann-Jerosch, H. & Rübel, E. (1912) *Die Einteilung der Pflantzen-gesellschaften nach ökologisch-physiolognomischen Geseichtspunkten*. W. Engelmann, Leipzig

development in succession was dependant on the mineral nutrient status of the system during the discussion session of a conference on the ecology of quarries (Davis, 1982).

Variation in the distribution of species and communities recorded on the bings was explained by measured variables of the chemical (14% explained variance) and the physical (14% explained variance) environment (Chapter Four, section 4.5). The total variability explained by all of the measured variables was 25%, indicating that the physical and chemical environmental factors were each explaining discrete variance in the composition of the vegetation. Management, including no management, was the factor that most influenced the distribution of species (Chapter Four, Figure 4.6) and the importance of this will be discussed in Section 7.4.

The detailed study of nine common species recorded in the bing vegetation showed that the correlations between seed production and viability, dispersal mechanisms and plant height explain additional variance at the scale of individual species (Chapter Five) and independently contribute to their distribution. Dispersal mechanisms are particularly important to colonisation of the bings because seeds have to be dispersed through space, often over large distances, rather than through time as would be the case in a secondary succession with a long established seedbank. Seed dispersal has long been recognised as a central mechanism of plant species distribution (Gleason, 1926) yet as recently as the 1990's research into dispersal mechanisms in plant and animal species was considered to be "nature study" and not worthy of funding (Miles and Walton, 1993). The urgent need for better data, particularly from the tails of seed dispersal curves where long-distance dispersal can be measured, is recognised as a key requirement to the understanding of colonisation of islands (Cain *et al.*, 2000) and other fragmented habitats (Eriksson, 2000). The limited data collected from this study will not add significantly to the gap in ecological knowledge of long range dispersal but reiterates the need for extensive research in this field.

Examination of the findings from this study as a whole established that the measured environmental factors were influential on vegetation succession at different levels of

spatial scale: altitude and aspect at the largest (bing) scale; management, bare ground, angle of slope and soil chemistry at the intermediate (within site) scale; dispersal, seed productivity and plant morphology at the smallest (individual/species) scale.

A conceptual model of the mechanisms and processes of vegetation succession on the West Lothian oil-shale bings was constructed with a combined hierarchical and modular structure representing each of the levels and the interaction of the components within them (Chapter Six). The model was comparable with general models of succession from literature as described in Chapter Six (Clements, 1916; Watt, 1947; Connell & Slater, 1977). The model of bing colonisation also describes the primary successional vegetation developing on volcanoes, sand dunes and other large isolated mounds of substrate that differ from the surrounding landscape. The plant associations and species recorded on the West Lothian bings can therefore be used to exemplify the mechanisms and processes of vegetation dynamics in other similar sites.

7.2 Indicator Species

Vascular plants are considered to be the most useful indicator species for identification of habitat quality: mammals and birds are too mobile and lower plants are often too difficult to identify in the field (Rose, 1999). An example of this is the method of assessing woodland flora using indicator species (Peterkin, 1974) that was adopted by the Nature Conservancy Council in the 1980's to identify ancient and semi-natural woodland habitats that should be protected. The Forestry Commission has recently adopted an ecological system of classification (ESC) of British forests based on ground vegetation and humus type as indicators of soil nutrient regime (Wilson *et al.*, 2001).

In the present study the Ellenberg indicator values of light, moisture, reaction and nitrogen allocated to individual plant species (Hill *et al.*, 1999) were employed to predict the likely physical and chemical environment on the shale bings. Individual species recorded on the bings that were limited by the angle of slope in a quadrat, for

example, or the by available nutrients in the substrate were described in Chapter Four. From the data created indicators of the physical environment (Table 7.1) and of the chemical environment (Table 7.2) can be identified.

Table 7.1 Indicators of the physical environment

Examples of species that can be used to indicate management, elevation, and slope on the bings. Many of them have been discussed in the text of Chapter 4. Asterisk (*) denotes species that are also indicators of chemical environment: dagger (†) denotes species that indicate more than one element of the physical environment.

Management regime		Elevation from base		Angle of slope	
managed	unmanaged	upper	lower	$< 30^{o}$	$\geq 30_{o}$
Agrostis gigantea	**Linum catharticum*	*Arenaria serpyllifolia*	*Medicago lupulina*	*Matricaria discoides*	**Arctium minus*
Alnus glutinosa	**Trifolium campestre*	*Cardamine hirsuta*	*Taraxacum officinale*	*Rhinanthus minor*	*Linaria vulgaris*
†Calluna vulgaris	*†Rosa canina*	*Festuca ovina*	*†Rosa canina*	*†Calluna vulgaris*	
†Poa trivialis	*†Rubus fruticosus*	*†Poa trivialis*	*†Rubus fruticosus*	**Stellaria media*	
†Potentilla erecta	*Senecio jacobea*	*†Potentilla erecta*	*Tussilago officinale*	*†Potentilla erecta*	
**Sanguisorba minor*		*Myosotis arvensis*	*Vicia hirsuta*	*Veronica persica*	

Table 7.2 Indicators of the chemical environment

Examples of species that can be used to indicate high pH and high measurements of available sodium (Na), phosphorus (P), potassium (K) and magnesium (Mg). Asterisk (*) denotes species that are also indicators of physical environment

pH	Na	P	Mg
**Medicago lupulina*	**Linum catharticum*	*Chamerion angustifolium*	**Arctium minus*
Sagina procumbens	*Tragopogon pratensis*	*Hesperis matronalis*	**Sanguisorba minor*
**Stellaria media*	**Trifolium campestre*		
Tripleurospermum inodorum	*Lotus corniculatus*		

The indicators of managed bings are predominantly species that are known to be planted, from management records (West Lothian Council, various), or heathland species that have established on sites in close proximity to large surrounding areas of heath (Chapter Four). The indicators of unmanaged bings are all species that are frequently recorded in the surrounding landscape, *Linum catharticum, Trifolium*

campestre, *Rosa canina*, *Rubus fruticosus* and *Senecio jacobea* (Smith *et al.*, 2002). *L. catharticum* and *T. campestre* also indicate high levels of sodium and could be important indicator species within management regimes.

Several of the species are indicative of more than one component of the physical environment and others are also indicators of high levels of nutrients within the chemical environment. The indicator value of these species are only expected to be relevant within the bing habitat and are possibly only valid in the eight bings that have been surveyed in this study however the generality of the association needs to be tested on other sites.

7.3 Transient and Transitory Species

Transients are plant species that do not persist within a community, whose seeds invade an ecosystem and germinate, and which establish but do not survive to reproduce (sometimes described as ephemerals). Transients are often relatively abundant species from nearby ecosystems that are unsuited to the physical and/or chemical conditions in their new environment. *Chaenorhinum minus* and *Galeopsis tetrahit*, for example, are annual ruderals found in the surrounding agricultural landscape that were recorded as occasional individuals on bare ground on newly managed bings. There was no evidence of successful reproduction, seedlings or small groups of individuals, and the individuals rapidly surrender to desiccation in the free draining open environment. The transient species are likely to be important in the development and maintenance of the ecosystem (Grime, 1998) by adding nutrients and organic matter to the soil. They are representative of the assortment of potential later colonisers and are important to the continuing biodiversity of a community in later successional stages. They may eventually reappear as established components of the vegetation when substrate or other environmental conditions change.

Transitory species are species that form an integral part of one or more of the early stages of succession. They reproduce and are well adapted to the initial conditions of the new environment. However as the ecosystem develops they are less able to

compete with new invaders, or are unable to adapt to changes in the physics and chemistry of the developing substrate. In the unmanaged bing environment these are represented by species like *Senecio viscosus* and *Reseda luteola* that are limited to areas of the bing where continuous disturbance or steep slopes maintain the conditions similar to those found in early successional stages with low vegetation cover and little competition from more competitive species. These are species of 'no fixed abode' that survive by 'island hopping' from one disturbed site to the next.

So-called exotic or non-native species also have to be considered in this section. Several garden escapes have been recorded on the bings and are well established on many sites. *Papaver somniferum* is one such species and can also be found on other man made sites, including the many roundabouts in Livingston (pers. obs.). Species like this may become a permanent component of plant assemblages on the bings and could form part of an established novel community type. Many environmentalists and ecological managers may consider that these are not natural and should therefore be discouraged, but having originated in a human-created habitat they can scarcely be considered as alien or introduced. Smith (2003) highlights the example of *Chamerion angustifolium*, a species that is recognised as native throughout Britain by the New Atlas of the British and Irish Flora (Preston *et al.*, 2002) and other floras (Stace, 1997; Clapham *et al.*, 1993; Rose, 1981) but was regarded as a garden escape by the county flora writers of Worcestershire (Amphlett and Rea, 1909) and Derbyshire (Linton, 1903) at the beginning of last century. Several of the other species recorded on the bings may also be of dubious origin (Lousley, 1953):

Matricaria matricarioides - First recorded in Britain in 1871 and only becoming widespread after the invention of the patterned tread of motor tyres (Lousley, 1953)

Veronica persica – first recorded @ 1820 and extending throughout Britain within 50 years despite its large seed size (Preston *et al.*, 2002)

Senecio viscosus – possibly only native as far north as Belgium on the continent and first recorded in Britain in 1660 (Preston *et al.*, 2002)

Acer pseudoplatanus – a naturalised introduction that is considered to be displacing native woodland species in Scotland (along with *Fagus sylvaticus*)

These and other exotics can pose a major dilemma to ecologists, botanists and land managers, especially when they are establishing on post-industrial waste land that has to be managed: should they be encouraged as an integral part of a novel vegetation type or treated as undesirables, alien species that should be removed for fear that they spread uncontrollably throughout the surrounding landscape.

7.4 Restoration and Management

Whatever the type of site, a damaged area of natural ecological value or an urban landfill site, there must be a clear plan of what the site is to be managed for, a specific objective and an end product that the manager intends to achieve.

Restoration and management of spoil waste is not a new concept and Oxenham (1966) describes the outcome of a planting regime 10 years earlier on Croxdale spoil heap near Durham. Restoration policy at this time (1956) followed a standard recipe of reducing the height and gradient of the heap, rounding peaks and ridges, covering with topsoil, applying fertilizers (liberally) and sowing with commercial grass mix. On low lying heaps trees, usually birch and alder, were planted directly into the spoil at the bottom of the heap without any amelioration. The sole purpose was "to obtain a satisfactory visual effect" (Oxenham, 1966). A great deal of restoration work currently being carried out continues to adhere to these fifty-year old policies and examples can be seen in some of the privately owned shale bings near Broxburn: Stankards and Green Bing (Appendix 1). The end product is species poor and visually boring.

Management decisions on the restoration of the bings and similar sites are often considered to be constrained by available sources of funding but frequently the real constraints on restoration managers are imposed by an unrealistic public perception of what post industrial and other waste sites should be restored to, and how quickly they should be restored. In Britain it is not the quantity of spoil that causes public concern but that it is situated in or near centres of population where it is seen as an immediate problem.

7.4.1 Natural reclamation vs. assisted management

Management has been shown to be a major factor in the distribution of both species and habitat types on the bings (Chapter Five). There have been a variety management regimes practised on different bing sites ranging from no management (Greendykes and Mid Breich) to complete reshaping and extensively planned seeding and replanting with carefully selected species (Oakbank and Addiewell north). The effects of management on the distribution of individual species and habitats have been discussed in Section 7.2 and Chapter Four.

Ecological management is often discussed in terms of succession, stability and diversity based on communities being in equilibrium, but serious consideration has to be given to the idea that there may be no such thing as equilibrium in practical terms. Natural colonisation of a site will depend on soil type and climate; stability if it occurs, will depend on time scale and disturbance. Restoration sites are often totally different from their surroundings. A pit bing or a small woodland that rises like an island in a sea of agricultural land follows the theory of island biogeography (Macarthur and Wilson, 2001). The rate of colonisation by new species will decrease as the total number of species on the island increases. A larger area will have a wider range of habitats; therefore potentially more species (Holt, 1992). In addition man-made sites in particular often provide a receptive substrate for seed rain that is very different in physical and chemical structure from the surrounding land. Seeds of species that would otherwise be unsuited to local soil conditions find refuge in these sites and add to the local biodiversity (Zhang *et al.*, 2001). The characteristically poor flora associated with many industrial spoil sites is more likely to be due to their isolation from similar habitats than to any deficiencies of the substrate (Miles and Walton, 1993).

The most diverse natural communities are not necessarily the oldest, nor are they the youngest. Maximum species levels occur when there is a small amount of disturbance. The best way to manage for rare species and biodiversity is not to enclose a site to keep everything out. Bings should not immediately be fenced off to minimise disturbance. The *status quo* should be maintained allowing free access to

the public (including off-road vehicles), as this is a major factor in determining the disturbed and diverse habitat conditions that maintain the complexity of vegetation. Their high species diversity can only be maintained if there is low productivity of biomass. All of the situations that restoration managers try to prevent, low nutrient availability, grazing, trampling, offroad biking, tend to increase diversity and have resulted in the particular flora that has arisen on the bings. Of course if there is too much of any kind of disturbance you will lose both diversity and habitat. Management plans have to strike a balance.

"No management" is often not recognised as an option by restoration managers because natural establishment of vegetation is considered to be too slow and the outcome can not be guaranteed. A cynic might suggest that it is also because managers are unlikely to be offered payment for recommending that nothing should be done. By using methods of observation and deduction it is possible to obtain a very full description of plant succession. Nature's "experiments" are replicated all over the world, often on a vast scale, yet ecologists are continually forced into conducting inefficient and ineffective trials and small-scale manipulative experiments to satisfy funding bodies. A major benefit of standing back and allowing nature to run its course is that there are no monetary costs involved.

The early invasion of woody species onto the bare soil of industrial waste is not unusual (Davis, 1982). Many pioneer tree species are excellent primary colonisers as can be seen in the impressive birch woodland at the base of Mid Breich. Bings that have not been managed were also noted to support species that were not recorded on managed sites and *vice versa.* Conservationists and managers however have to be prepared to accept loss of species as well as gains if successional habitats like the bings are to be maintained and managed. Succession is a dynamic process that cannot be preserved. The species involved in the colonisation of a newly formed bing (or any other primary site) can not all be retained permanently, even in areas of continuous disturbance.

When species from this study were compared with species recorded in a comprehensive and comparable database of species recorded in post-industrial

habitats of the Sheffield region (Grime *et al.*, 1988) their within site distributions were found to be mostly limited by the same environmental factors. However there were several species that were frequent, and limited in distribution, in the bing habitats that were not recorded in the Sheffield survey. *Reseda luteola*, *Cerastium glomeratum* and *Veronica serpyllifolia* were representative of areas with more than 30% bare ground on shale bings but not recorded in Sheffield. These are considered to be widespread species in West Lothian (Smith *et al.*, 2002): *V. serpyllifolia* is as common in the county as *V. chamaedrys* although *R. luteola* and *C. glomeratum* are limited in habitat. The two species most restricted by aspect on the shale bings, *Luzula multiflora* and *Peltigera canina*, have no individual records in the Sheffield flora, nor has *Papaver dubium*. *Luzula multiflora* is grouped with *L. campestris* and treated as one species by Grime *et al.* (1988) whereas in West Lothian the two species, although both common, have very different habitats with only *L. multiflora* recorded on bings (Smith *et al.*, 2002). *P. dubium* is recorded on bings in West Lothian, and although similar in habit, *P. rhoeas* is not, despite being common in many other sites (Smith *et al.*, 2002).

The distribution limits of common species are rarely considered in assisted management, yet recognising that even locally common species will not always be suited to a site that is being restored should be an important part of management plans. The nine common species selected for detailed examination in this study have been consistently referred to in other studies of the colonisation of waste sites (Chapter 5; Grime, 1986) making them, potentially, an integral component of restoration policy.

Michael Usher (1993) promoted the creation of complete communities as an alternative to planting trees and hoping that all other organisms will arrive naturally. This was an exciting and innovative approach to assisted succession and land reclamation but unwittingly supports the current trend for constructing vegetation types using Rodwell's volumes (1991a; 1991b; 1992; 1995; 2000) as a series of recipe books: certainly not the use that Rodwell intended for the National Vegetation Classification. The modern ideal that species will march in serried ranks to fulfil the

criteria for NVC type CG5, for example, if the "correct" habitat conditions are provided is a dangerous and totally unrealistic concept.

The advantages and disadvantages of incorporating unassisted colonisation into the restoration of the extensive strip-mined brown coalfields of the Czech Republic are presented in a series of papers by Karel Prach and Petr Pyšek (1994; 1999; 2001; 2003) that exemplifies some of the considerable research that has been developed in Central Europe on the "spontaneous establishment" of vegetation on derelict sites (Table 7.3).

Table 7.3 Using natural invasion in restoration management

Summary of the advantages and disadvantages in using unassisted colonisation in the restoration of derelict sites in Central Europe (Prach and Pyšek, 2001)

Positive	Negative
Low cost	Succession may be arrested in early stages
Usually low cover of invasive species	Occasional seed sources of agricultural weeds
Often refugia for wildlife	Proximity to centres of population that can be sensitive to sources of allergenic pollens from grasses and trees
Usually higher natural value than artificially restored sites	Usually lower productive value than artificially restored sites
Often expansion of native woody species	

They conclude that natural succession can be relied upon in restoration projects except in the case of especially toxic substrates and that it is especially advantageous where the disturbed site is small and surrounded by natural vegetation. Prach and Pyšek (1994) describe successful colonisation in a series of 15 large sites by woody species after ten years of abandonment. Despite the larger scale of the spoil sites in Central Europe these observations support the findings of this study that there was no indication that lack of available nitrogen had any significant effect on invasion and establishment. The time scale of only ten years for these successful colonisations suggests that the continental climatic conditions in Central Europe are more conducive to rapid invasion than those in Central Scotland.

To retain biodiversity it is important to know as much as possible about the mechanisms and processes of colonisation in successful species before decisions are

made on any land management. The findings from studies of succession on man-made sites can be incorporated into the management of set aside, the inclusion of fallow fields in crop rotation and other conservation practices.

Changes in agricultural policies during the 20th century have caused habitat loss for many common weed species and although now an integral part of farm management most studies on set-aside effect on weed populations have been made in the USA (Marshall & Hopkins, 1990). In a UK study of abandoned arable land on chalk Graham and Hutchings (1988a; 1988b) reported that there was insufficient quantity and variation of propagules in the seedbank and seed rain to recreate chalk grassland. The findings of this and other studies on derelict land suggest that this may be a pessimistic view of the long-term ability of species to survive in seedbanks or as transitory species in other habitats. The diversity of species still abounds although individual species are not necessarily in the habitats where they once were. Many agricultural species have found their way onto the West Lothian shale bings and examples of *Agrostemma githago* (corncockle) and *Centaurea cyanus* (cornflower) are frequently being recorded on road verges in many parts of Britain (Plantlife, 2004).

7.5 Bings and Biodiversity

Biodiversity is not only about rare and exotic species but also about the variety of common species and communities that are contributing to the quality of the landscape. Greenwood and Gemmell, (1978) consistently recorded regionally rare and localised species, particularly *Dactylorhiza purpurella* and *D. praetermissa*, in 25 derelict industrial land sites in Lancashire (Watsonian vice counties 59, S. Lancs., and 60, W. Lancs.). Like the bings these were base-rich man-made habitats with a list of associated flora including *Holcus lanatus*, *Centaurea nigra* and *Plantago lanceolata,* that were noted as being constant to all sites, and also the unexpected colonisation by the coastal species *Anthyllis vulneraria*, a very similar scenario to that recorded on the oil-shale waste.

The oil-shale bings form island refugia for wildlife in the primarily agricultural and urban landscape of West Lothian. The extent of floral biodiversity has been documented throughout this study and formally recorded at the Scottish Wildlife Trust's North Addiewell Nature Reserve and on the bing at Faucheldean, which are both protected from development and which support several plant species not found elsewhere in the county (Sheldon, 1997). Five Sisters and Greendykes bings, which are scheduled national monuments, also provide habitats for a wide range of locally threatened flora and fauna. All of the bings are home to many common plants and animals that are becoming increasingly marginalised by demands for more land for new housing and changes in farming methods: the nine "weeds" that were studied in Chapter Five for example.

7.5.1 Locally Rare Fauna

Although this study concentrated primarily on the succession of vegetation on the bings locally rare animals were often noted, especially on early morning field visits. These included *Lepus europaeus* (hare) on Greendykes and Clapperton, *Lagopus lagopus scotticus* (red grouse) on Greendykes, *Meles meles* (badger) on Oakbank, *Alauda arvensis* (sky lark) on Greendykes and *Polyommatus icarus* (common blue butterfly) on Oakbank. The bings visited were also home to foxes (*Vulpes vulpes*), often seen in family groups, suggesting that many unobserved fauna are also inhabiting the sites (pers. obs.).

Formal recording of birds has been carried out at Addiewell bing by the Scottish Wildlife Trust by two independent methods, the Common Bird Census and Point Count Methodology (Collinson and McLean, 1997). Forty seven species were recorded during 1997, including 30 species with permanent breeding territories.

Insect records from Addiewell bing tend to be of showy species, mainly butterflies (Table 7.1), and include *Aphantopus hyperantus* (ringlet butterfly), very rare in central Scotland, and a first recording of *Adalia decempunctata* (ten-spot ladybird) in the county (Collinson and McLean, 1997). More formal insect recordings have been carried out but are not specific to the bings.

Table 7.4 Insects recorded at Addiewell Bing

*The notable species recorded in 1997 on Addiewell Bing adapted from Collinson and McLean (1997). Binomials from Chinery (1993) or *Linssen (1987).*

Butterflies	Butterflies	Other insects
Aglais urticae L.	*Pieris rapae* L.	*Deilephila elpenor* L.
Small tortoiseshell	Small white	Elephant hawkmoth
Anthocharis cardamines L.	*Pieris brassicae* L.	*Enallagma cyathigerum**
Orange tip	Large white	Common blue damselfly
Vanessa atalanta L.	*Maniola jurtina* L.	*Adalia decempunctata* L.
Red admiral	Meadow brown	Ten-spot ladybird
Lycaena phlaeas L.	*Aphantopus hyperantus* L.	*Nicrophorus* sp.
Small copper	Ringlet	Sexton beetle

7.5.2 Locally Rare Flora

There are many records of locally and nationally rare flora on the bings. As a habitat they are consistently recorded as sole or main habitats for species in local floras (Muscott, 1989; McKean, 1989; Smith *et al.*, 2002) and Muscott's (1989) "A Checklist of the Flowering Plants and Ferns of West Lothian" has a drawing of Niddry bing on the front cover.

The rarity of *Senecio viscosus* (sticky groundsel), *Anthyllus vulneraria* (kidney vetch), *Sedum acre* (bitter stonecrop) and *Artemesia absinthum* (wormwood) at a local level have been alluded to in earlier chapters and *Veronica polita* (grey field-speedwell) and *Chaenorhinum minus* (small toadflax), each recorded only once in this study, are recognised as very rare in West Lothian (Sheldon, 1997; Muscott, 1989).

Faucheldean bing is noted for colonies of the clubmosses *Lycopodium clavatum* (stag's-horn clubmoss) and *Diphastrum alpinum* (alpine clubmoss). Both species are very rare in West Lothian (Smith *et al.*, 2002; Muscott, 1989: Steven and Long, 1989) and are more usually associated with montane habitats.

Many of the rarest species recorded on the bings, however, are bryophytes and lichens. B.J. Coppins (Smith *et al.*, 2002, Chapter 8) describes a small population of the montane lichen *Stereocaulon saxatile* on Addiewell bing and extensive colonies of three species (*S. leucophaeopsis*, *S. nanodes* and *S. pileatum*) on Philpstoun bing that are otherwise exceedingly rare locally.

Almost half of all the bryophytes that are recorded in Britain are present in the Lothians yet shale bing habits are identified as important to the bryophyte flora of the three counties by D.F Chamberlain (Smith *et al.*, 2002, chapter 9). *Buxbaumia aphylla* Hedw. is a rare moss in Britain that has been recorded in sizeable populations only on bing debris in central Scotland (Steven and Long, 1989). Its persistence at Addiewell bing for more than 35 years is remarkable for a species that is usually considered to be ephemeral in natural habitats (Crum, 1973) identifying the destruction and landscaping of the bings as a severe threat to this species nationally.

7.5.3 West Lothian Biodiversity Action Plan

The concept that post-industrial sites and undeveloped land are important to biodiversity and conservation is not new and many Sites of Special Scientific Interest (SSSIs) are quarries and mineral workings (Bradshaw and Chadwick, 1980). It is therefore not surprising to find that the importance of the shale bings is recognised by the local authority. The Local Biodiversity Action Plan for West Lothian is being developed around eight habitats that are of particular importance (Sheldon, 1997): "Oil-shale bings" is one of these habitats. The bings are recognised as "distinctive to the area and having unique assemblages of wildlife which need more recognition and conservation..... they must now be recognised as contributing an important element of diversity".

A selection of native species from the list of 1250 species that have been identified by the government as requiring attention at national (United Kingdom) level have been selected for inclusion in the "100 target species list for West Lothian" (Sheldon, 1997), because they are either:

1) internationally rare or threatened,
2) locally rare or threatened,
3) recently extinct in West Lothian but should be present,
4) locally important or
5) give West Lothian its distinct character.

There are ten plant species from this list that are unique to the bing habitat or have the bings as their main habitat (Table 7.5). Many others species are recorded on the

bings as well as in their main habitat, including *Meles meles* (badger), *Lepus europaeus* (brown hare), *Capreolus capreolus* (roe deer), *Alauda arvensis* (skylark) and *Selaginella selaginoides* (lesser clubmoss) (personal observation).

Table 7.5 Bing species in the local biodiversity action plan

Ten of the plant species that have been selected to represent the bing habitat in the West Lothian local biodiversity action plan

Species name	Common name	Why selected
Trifolium striatum	Knotted clover	Very rare in central belt and characteristic of shale bings
Betula pubescens	Downy birch	Characteristic of shale bings
Briza media	Quaking grass	Locally rare and characteristic of basic soil
Orchis mascula	Early purple orchid	Scarce and diminishing
Epipactis youngiana	Young's helleborine	Globally rare, notifiable under the wildlife and countryside act 1981 and only recorded on bings
Gnaphalium sylvaticum	Heath cudweed	Nationally scarce, very rare in the Central belt and only on recorded on shale bings
Platanthera chlorantha	Greater butterfly orchid	Scarce and characteristic of basic soil
Rhinanathus minor	Yellow rattle	Typical of West Lothian flora
Lycopodium clavatum	Stag's horn clubmoss	Locally scarce and characteristic of shale bings
Buxbaumia aphylla		Only on shale bings

7.6 'Plant Life of Edinburgh and the Lothians' and 'Atlas 2000'

Plant Life of Edinburgh and the Lothians (Smith *et al.*, 2002) has frequently been cited as a reference in earlier chapters. As part of the recording team for this volume I was responsible for collecting the data in several of the survey squares in and around West Lothian prior to embarking on this thesis so have independently supplied some of the confirmatory references to species distribution.

The timing of the base line survey work of the thesis coincided with the national collection of field data for the Atlas 2000 project that led to the publication of the New Atlas of the British and Irish Flora (Preston *et al.*, 2002). The relevant plant species lists and site information were recorded on standard BSBI field cards and sent to Jackie Muscott and Douglas McKean, the BSBI recorders for the Watsonian

Vice Counties of West Lothian and Mid Lothian respectively. The data provided resulted in two new species records for Mid Lothian (VC 83, Edinburgh) and six new species records plus four updates for West Lothian (VC 84 Linlithgow). The anomaly of the two recording Vice Counties falling within the area now known as West Lothian occurs because of the numerous political county boundary changes over the last 100 years as mentioned in Chapter Three.

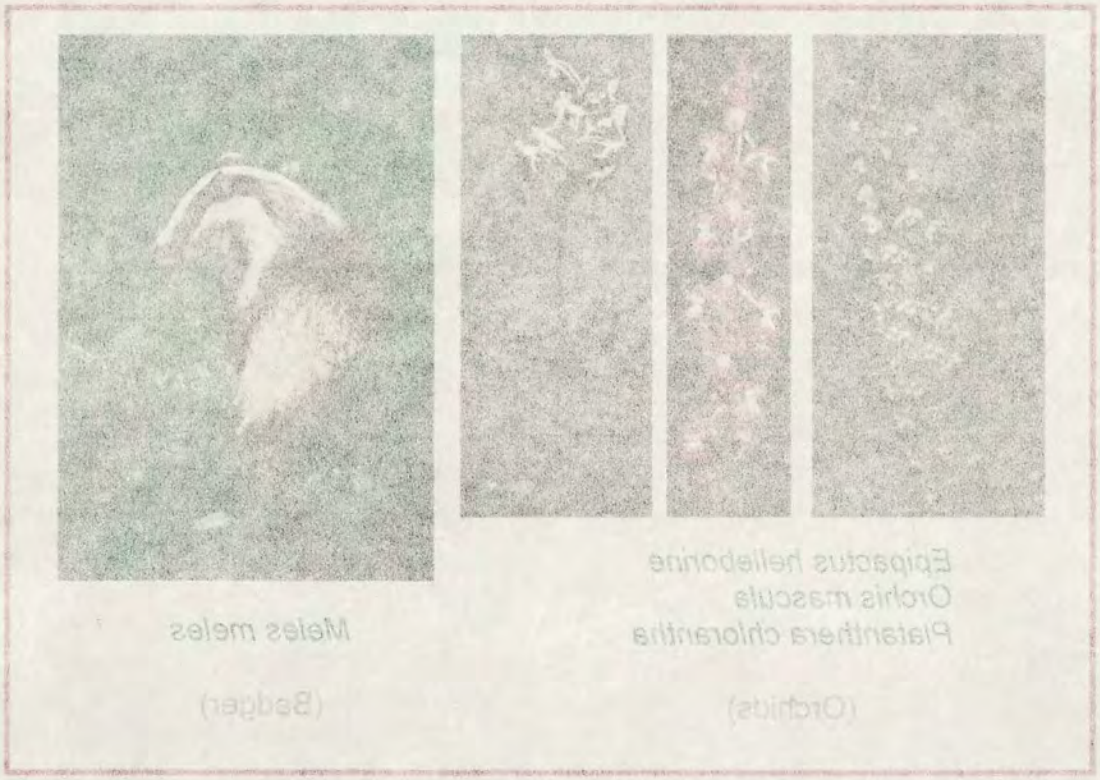
7.7 Conclusion

The oil shale bings of West Lothian have accrued considerable heritage value. The industrial exploitation of oil-bearing rocks has created a unique landscape with its own distinctive flora and fauna. The ecology and biodiversity of the bing sites make them ideal for describing and monitoring the processes and mechanisms of vegetation dynamics over a wide range of conditions. They provide an insight into the best-suited ecosystem structures for similar sites in other countries.

Figure 7.1 Examples of local biodiversity

Three orchids (photographs from Bioimages, undated) and a badger photographed on the West Lothian oil-shale bings at the base of Oakbank

Shale bings are of great ecological and scientific importance as examples of primary succession. They provide a refuge for locally rare species, both plant and animal, in an agricultural landscape and are therefore important to conservation and increased local biodiversity (Figure 7.1). The industries that built the bings also built the society and community structure of the existing human populations and initially provided most of the housing for them. The bings are now much used recreational sites for the population of West Lothian. We should rejoice in their infinite variety and constant dynamism.



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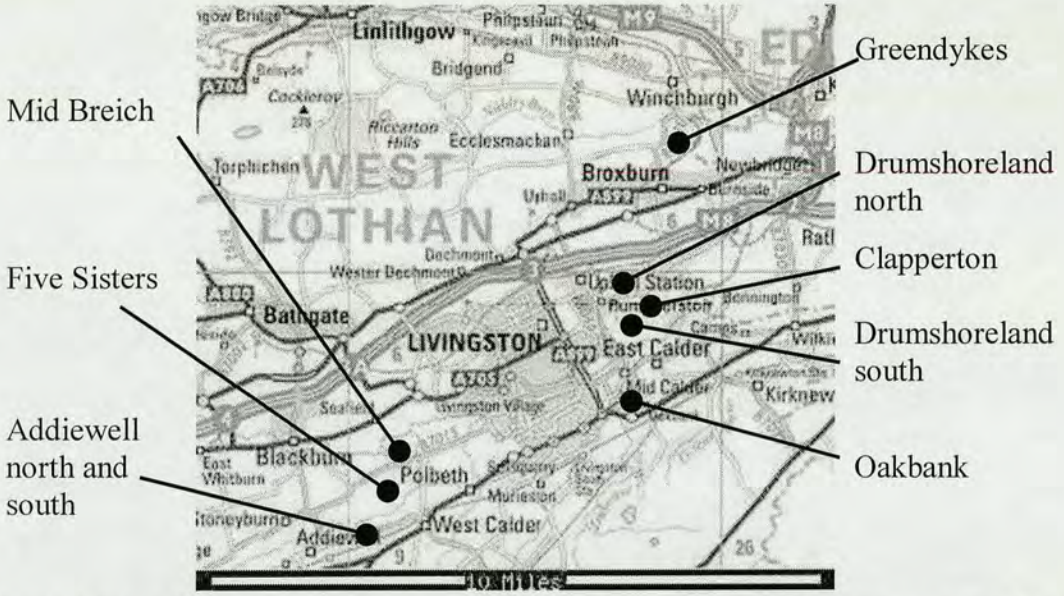
APPENDICES

Appendix 1 Site descriptions

Descriptions, maps and locations are given for all of the 19 bings in West Lothian at the time of writing (2004). Bings 1-8 are the sites used for data collection and the remaining bings are referred to in this thesis. The tabulated data are adapted from The Lothians Regional Survey and Plan (Development Department, 1966) and West Lothian Council Archive material (various dates). Heights are adjusted to the nearest metre and areas to the nearest hectare. Asterisks (*) denote bings where the height and altitude measurements are pre-management.
The descriptive notes are compiled from a wide range of sources but mainly from John Sheldon (pers. comm.), West Lothian Council archives and observations noted during the 25 years I have lived in the county. Information is patchy and incomplete, as it is more readily available for some bings than others. The accompanying maps are adapted from the Multimap service (http://www.multimap.com). Map 1 gives an overview of the position of the main bings used in this study.

Site name	Grid reference	Close date	Bing height	Basal area	Summit altitude
Addiewell north	NT [(3)]002 [(6)]631	1932	9m	12ha	180m
Addiewell south	NT [(3)]005 [(6)]627	1932	30m	30ha	210m
Greendykes	NT [(3)]087 [(6)]736	1925	95m	33ha	185m
Drumshoreland north*	NT [(3)]075 [(6)]700	1925	61m	26ha	180m
Clapperton*	NT [(3)]079 [(6)]697	1925	38m	11ha	160m
Drumshoreland south*	NT [(3)]078 [(6)]695	1925	61m	7ha	180m
Oakbank	NT [(3)]076 [(6)]664	1932	46m	13ha	175m
Mid Breich	NT [(3)]009 [(6)]646	1915	12m	4ha	145m
Five Sisters	NT [(3)]009 [(6)]641	1962	91m	17ha	240m
Faucheldean	NT [(3)]085 [(6)]742	1925	31m	9ha	120m
Niddry*	NT [(3)]097 [(6)]746	1961	61m	8ha	150m
Albyn	NT [(3)]085 [(6)]729	1925	46m	6ha	135m
Green Bing*	NT [(3)]070 [(6)]710	1920	61m	9ha	160m
Stankards*	NT [(3)]063 [(6)]711	1920	61m	10ha	160m
Seafield	NT [(3)]005 [(6)]667	1932	53m	12ha	200m
Deans	NT [(3)]015 [(6)]685	1946	76m	74ha	175m
Philpstoun north	NT [(3)]057 [(6)]769	1932	30m	10ha	100m
Philpstoun south	NT [(3)]056 [(6)]765	1932	53m	27ha	125m
Bridgend	NT [(3)]037 [(6)]758	1932	24m	12ha	125m



Map 1 The positions of the principal bings in relation to the towns and transport routes in West Lothian county.

Addiewell north (Map 2) lies next to the Breich Water, to the north of the B792 between the towns of Addiewell and West Calder. Extraction ceased in 1932 and the bing remained undisturbed for 50 years. During this period natural colonisation by plants and animals began. Reshaping work was carried out to prevent the bing from falling into the Breich Water and many thousands of native and other trees were planted to stabilise the soil (Collinson and McLean, 1997; WLC Archives). This resulted in a diverse mosaic of habitats, demonstrating the processes of colonisation and succession on a sterile substrate. In 1987 The Scottish Wildlife Trust (SWT) took responsibility for the management of Addiewell North bing from the (then) Lothian Regional Council (Collinson and McLean, 1997). The management programme includes gradual removal of non-native species, mainly *Pinus contorta* Douglas ex. Louden (lodgepole pine) which were planted during the rehabilitation of the site, to make way for *Populus tremula* L. (aspen), *Corylus avellana* L. (hazel), *Quercus spp.* (oak), *Viburnum lantana* L. (wayfarer) and *Betula pendula* Roth (silver birch). There is all year round public access to the site and SWT hold an annual open day to encourage and inform visitors (*Collinson, 1997*).

Addiewell south (Map 2) lies to the south of the B792 between the towns of Addiewell and West Calder. The history of this bing is similar to its near neighbour,

Addiewell North. From the time excavations ceased until 1990 the bing remained unmanaged and plant and animal colonisation occurred naturally. In 1991 Lothian Region Council, in conjunction with the Scottish Development Agency began a one off, rehabilitation management plan on the site. The plan included a general site clearance, drainage and fencing programme, maintenance of paths and landscaping. At the same time the main mineshaft was capped and there was extensive removal of blaes from the south and west sides of the site. Approximately half the area (15.8ha) was ripped, fertilised and seeded using commercial grass seed mixtures (species not specified) and the remaining area was planted with several thousand trees and shrubs (mainly native species). There is no record of any further management action (W. L. C. archives) but the cleared area has been designated as the site for a new prison (Edinburgh Evening News, 5th and 30th January 2004). The remaining east and north section of the bing is an amenity site, used mainly by local residents for dog-walking and is owned by West Lothian Council.

Map 2 Addiewell north and south bings

Map 3 From north to south: Niddry Faucheldean and Greendykes

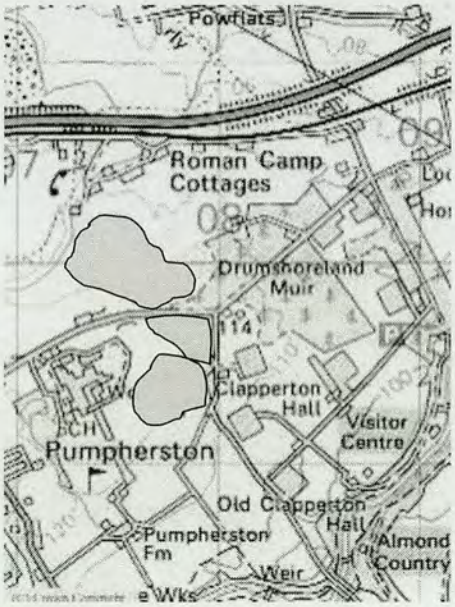
Greendykes also known as Broxburn bing (Map 3), is one of the largest and highest of the bings and lies to the south of the B8020 between Broxburn and Winchburgh. It is highly visible from the M8 motorway, making it one of the most conspicuous landmarks in the county. The ownership of the bing is shared between West Lothian Council (south) and Hopetoun Estates (north). There has been no active

management of the site since extraction in the area ended in 1925. The site has open access and is popular with off road motor cyclists and mountain bikers. This causes some localised erosion to the substrate, but on the whole the damage is limited to well defined paths. Colonisation by plants and animals is wholly natural and in some areas is well developed.

Drumshoreland north (Map 4) Blaes has been extracted from the north of this bing and there is currently (2004) considerable reshaping of the slopes to stabilise the remaining structure. The vegetation at the base has mostly been undisturbed but has been removed from large areas of the middle slopes, top and plateau leaving new sites for colonisation.

Clapperton (Map 4) was reshaped and planted by a private company shortly before the survey work for this study took place. As with many managed sites the base vegetation remained undisturbed during the management.

Drumshoreland south (Map 4) has recently (1998/99) undergone considerable reshaping and planting. It now stands approximately 40 m high compared to its original 61m.



Map 4 From north to south: Drumshoreland north, Clapperton, and Drumshoreland south

Map 5 Oakbank

Oakbank (Map 5) lies beside a small ex-mining village of the same name, situated toward the eastern boundary of the present (2004) political county of West Lothian, however it is on the north west boundary of Vice County 83, Midlothian.

The shale bing at Oakbank contains 5 million cubic yards (3,825,000 cubic metres) of burnt shale in a heap with steep sides and a flat top (W L C archives). The Oakbank bing was reclaimed for amenity use after 1988 by Lothian Regional Council and is now owned and maintained by West Lothian District Council. A continuous band of woodland, from 25 m to 100 m wide, has been established in the middle to upper slopes using:

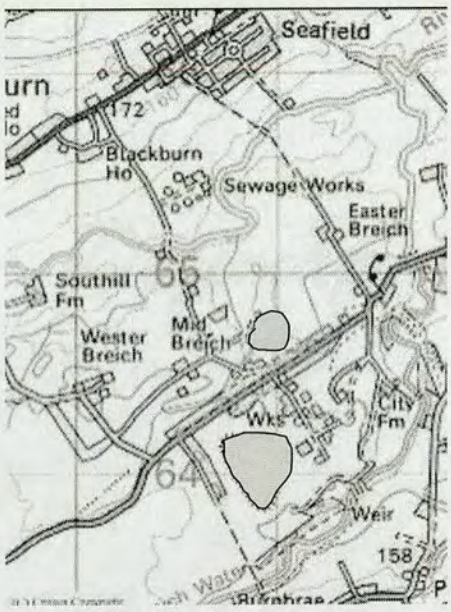
1 .Woodland planting at 1x1 m density (*Alnus glutinosa, Acer pseudoplatanus, Betula pendula, Corylus avellana, Crataegus monogyna, Fagus sylvatica, Fraxinus excelsior, Larix x eurolepis, Pinus sylvestris, Pinus contorta, Pinus nigra austriaca* and *Quercus petraea*).

2. Edge planting at 1x1 m density (*Corylus avellana, Crataegus monogyna, Ligustrum vulgare* and *Salix caprea*) with central planting at 2x2 m density (*Acer pseudoplatanus, Alnus glutinosa, Betula pendula* and *Prunus avium*).

There have been several small irregular areas (approximately one tenth of a hectare each) of tree and shrub seeding. Grass and wild flower seed mix has been sown on the summit and three areas of lower slopes resulting in well established 'meadowland'. There has been retention of existing vegetation on the steep north and west facing slopes of the River Almond valley immediately below the bing proper (W. L. C. archives).

Mid Breich (Map 6) is the smallest remaining shale bing in West Lothian. It has been unused since before 1915 (Ordnance Survey, 1915) and has not been reclaimed or planted since that time. It is situated just inside the south boundary of the botanical vice county of West Lothian between the River Almond and Murieston Water. The bing was originally conical with a rounded summit, however a large area of the south side of the bing has been excavated at some stage in its history leaving behind a horseshoe shaped structure. As the vegetation in and around this excavated area is well established, including some birch woodland, the bing has almost certainly not been managed for at least 50 years. Some areas at the base of the bing have been used as dumping areas for large items of household and garden refuse, and

there is a 'graveyard' for dead buses nestling against the western perimeter. This has all added to the diverse vegetation that has developed over this fascinating little bing.



Map 6 Mid Breich and Five Sisters

Five Sisters (Map 6), also known as Westwood Bing is the most striking of all the bings. Its five symmetrical peaks tower over the surrounding landscape and are clearly visible from Livingston, more than 5 miles away. The bing is in open agricultural land between Breich Water and the B7015. It has remained unmanaged since the closure of the mine workings but vegetation is still sparse on most of its slopes. It is however host to 'mountaineering' cattle that regularly lumber over its multiple summits.

Faucheldean (Map 3) has protected status because of the colonisation of the bing by several locally rare species of orchids and stag's – horn clubmoss. It lies north of the B8020 on the outskirts of Winchburgh, opposite the much larger Greendykes bing.

Niddry (Map 3) is located east of Winchburgh between the M9 and the railway. Blaes is currently (2004) being extracted from this bing. The ruins of Niddry Castle nestle at its base. This was where Mary Queen of Scots spent her first night of freedom after her daring escape from imprisonment in Loch Leven Castle (Keay and Keay, 1994).

Albyn (Map 3) can be found north of Broxburn where the Union Canal is bridged by the B8020. Most of it was removed, to raise the road over the canal and allow clear access for barges and pleasure boats, as part of the "Millennium Link" between the Union, and Forth and Clyde canals.

The Green Bing is on the outskirts of Pumpherston, one of the larger ex-mining towns in West Lothian. The bing is situated on the south side of the A89 (this was the main highway from Edinburgh to Glasgow before the advent of the M8 motorway). When extraction ceased in 1920 it stood 61 m high and covered 9 ha but was partly demolished and the shale used as landfill material for new housing estates in Broxburn (1999/2000). Its 'remains' are currently being reshaped and seeded.

Stankards is immediately adjacent to the Green Bing and has been remodelled, seeded and planted for use as an amenity area for the residents of nearby housing estates. Stankards covers 9.7 ha and its summit is now approximately 150 m above sea level, the height of the bing having been reduced to approximately 30 m since it was last used in 1920.

Seafield is situated north of the A705 and the village of Seafield. The bing site has been used by the local council for tipping household refuse at various times since 1959 and sewage sludge between 1989-90. Reclamation plans were drawn up in 1991 but the proposed work was never carried out.

Deans covers the largest area of all the remaining bings in West Lothian although it is not the highest. The bing is south of the M8, west of Deans, Livingston. It is now almost unnoticeable with rolling slopes covered in grass and scrub that look like a 'natural' land feature. It is now home to Deans bus depot.

Philpstoun north is situated 500 m east of the village of Philpstoun, between the railway line and the Union Canal, west of the B8046. This is the furthest north of the West Lothian bings.

Philpstoun south lies across the canal from its smaller namesake.

Bridgend can be found between the villages of Bridgend and Kingscavil on the north bank of the Haugh Burn.

Appendix 2 Combined species list from previous studies

Species name, authority, family and common name are listed for the 304 species recorded in previous studies (Maka,1995 ; Martin, 1992; Russell, 1971). Alternative species names have been included where these are in common use.

species	authority	family	common name
Acer platanoides	L.	ACERACEAE	Norway maple
Acer pseudoplatanus	L.	ACERACEAE	sycamore
Achillea millefolium	L.	ASTERACEAE	yarrow
Achillea ptarmica	L.	ASTERACEAE	sneezewort
Aegopodium podagraria	L.	APIACEAE	ground elder
Agropyron caninum (Elymus caninus)	(L.) Beauv.	POACEAE	bearded couch grass
Agropyron repens	(L.) Beauv.	POACEAE	couch grass
Agrostis stolonifera	L.	POACEAE	brown bent
Agrostis tenuis (A. capillaris)	Sibth.	POACEAE	common bent
Aira praecox	L.	POACEAE	early hair grass
Alchemilla filicalis	Buser	ROSACEAE	lady's mantle
Alisma plantago-aquatica	L.	ALISMATACEAE	water plantain
Allium ursinum	L.	LILIACEAE	ramsons
Alnus glutinosa	(L.) Gaertn.	BETULACEAE	alder
Alnus rubra	Bong.	BETULACEAE	red alder
Angelica sylvestris	L.	APIACEAE	wild angelica
Anthoxanthum odoratum	L.	POACEAE	sweet vernal grass
Anthriscus sylvestris	(L.) Hoffm.	APIACEAE	cow parsley
Anthyllis vulneraria	L.	FABACEAE	kidney vetch
Arabidopsis thaliana	(L.) Heynh.	BRASSICACEAE	thale cress
Arctium minus	(Hill) Bernh.	ASTERACEAE	lesser burdock
Arenaria serpyllifolia	L.	CARYOPHYLLACEAE	thyme leaved sandwort
Armoracia rusticana	P.Gaertn., B.Mey. & Schreb.	BRASSICACEAE	horse radish
Arrhenatherum elatius	(L.) Beauv. ex J. & C. Presl	POACEAE	false oat grass
Artemesia vulgaris	L.	ASTERACEAE	mugwort
Aster sp	L.	ASTERACEAE	michaelmas daisy
Athyrium filix-femina	(L.) Roth	ATHYRIACEAE	lady fern
Avena fatua	L.	POACEAE	common wild oat
Bellis perennis	L.	ASTERACEAE	daisy
Betula pendula	Roth.	BETULACEAE	silver birch
Betula pubescens	Ehrh.	BETULACEAE	downy birch
Blechnum spicant	(L.) Roth	BLECHNACEAE	hard fern
Botrychium lunaria	(L.) Sw.	OPHIOGLOSSACEAE	moonwort
Brassica napus	L.	BRASSICACEAE	rape
Brassica nigra	(L.) W.D.J. Koch	BRASSICACEAE	black mustard
Buxbaumia aphylla		BRYOPHYTA	
Calluna vulgaris	(L.) Hull	ERICACEAE	heather, ling
Caltha palustris	L.	RANUNCULACEAE	marsh marigold
Calystegia sepium	(L.) R. Br.	CONVOLVULACEAE	hedge bindweed
Calystegia sylvatica	(Kit.) Griseb.	CONVOLVULACEAE	large bindweed

species	authority	family	common name
Campanula latifolia	L.	CAMPANULACEAE	giant bellflower
Campanula rotundifolia	L.	CAMPANULACEAE	harebell
Capsella bursa-pastoris	(L.) Medik.	BRASSICACEAE	shepherd's purse
Cardamine hirsuta	L.	BRASSICACEAE	hairy bittercress
Carduus crispus (*C. acanthoides*)	L.	ASTERACEAE	welted thistle
Carex hirta	L.	CYPERACEAE	hairy sedge
Carex nigra	(L.) Reichard	CYPERACEAE	common sedge
Carex rostrata	Stokes	CYPERACEAE	bottle sedge
Carex viridula (*C. lepidocarpa*)	Michx.	CYPERACEAE	yellow sedge
Centaurea montana	L.	ASTERACEAE	perenniel cornflower
Centaurea nigra	L.	ASTERACEAE	black knapweed
Centaurea scabiosa	L.	ASTERACEAE	greater knapweed
Cerastium fontanum	Baumg.	CARYOPHYLLACEAE	common mouse-ear
Chaenorhinum minus	(L.) Lange	SCROPHULARIACEAE	small toadflax
Chamerion angustifolium	(L.) Holub	ONAGRACEAE	rosebay willowherb
Chenopodium album	L.	CHENOPODIACEAE	fat hen
Chrysanthemum segetum	L.	ASTERACEAE	corn marigold
Cicerbita macrophylla	(Willd.) Wallr.	ASTERACEAE	blue sow thistle
Cichorium intybus	L.	ASTERACEAE	chicory
Cirsium arvense	(L.) Scop.	ASTERACEAE	creeping thistle
Cirsium heterophyllum	(L.) Hill	ASTERACEAE	melancholy thistle
Cirsium palustre	(L.) Scop.	ASTERACEAE	marsh thistle
Cirsium vulgare	(Sari) Ten.	ASTERACEAE	spear thistle
Cladonia fimbriata		lichen	
Claytonia sibirica	L.	AIZOACEAE	pink purslane
Conium maculatum	L.	APIACEAE	hemlock
Conopodium majus	(Gouan) Loret	APIACEAE	pignut
Corylus avellana	L.	CORYLACEAE	hazel
Cotoneaster integrifolius	(Roxb.) G.Klotz	ROSACEAE	entire-leaved cotoneaster
Crataegus monogyna	Jacq.	ROSACEAE	hawthorn
Crepis capillaris	(L.) Wallr.	ASTERACEAE	smooth hawksbeard
Crepis paludosa	(L.) Moench	ASTERACEAE	marsh hawksbeard
Cruciata laevipes	Opiz	RUBIACEAE	crosswort
Cynosurus cristatus	L.	POACEAE	crested dog's tail
Cytisus scoparius	(L.) Link.	FABACEAE	broom
Dactylis glomerata	L.	POACEAE	cocksfoot
Dactylorhiza fuchsii	Druce	ORCHIDACEAE	common spotted orchid
Dactylorhiza maculata	L.	ORCHIDACEAE	heath orchid

species	authority	family	common name
Dactylorhiza purpurella	T. & T.A.Stephenson	ORCHIDACEAE	northern marsh orchid
Deschampsia caespitosa	(L.) Beauv.	POACEAE	tufted hair grass
Deschampsia flexuosa	(L.) Trin.	POACEAE	wavy hair grass
Digitalis purpurea	L.	SCROPHULARIACEAE	foxglove
Diphasiastrum alpinum (Diphasium alpinum)	(L.) Holub	LYCOPODIACEAE	alpine clubmoss
Dipsacus fullonum	L.	DIPSACEAE	teasel
Dryopteris dilitata	(Hoffm.) A.Gray	ASPIDACEAE	common buckler fern
Dryopteris filix-mas	(L.) Schott	ASPIDACEAE	male fern
Epilobium hirsutum	L.	ONAGRACEAE	great willowherb
Epilobium montanum	L.	ONAGRACEAE	broad-leaved willowherb
Epilobium palustre	L.	ONAGRACEAE	marsh willowherb
Epipactis helleborine	(L.) Crante	ORCHIDACEAE	broad-leaved helliborine
Equisetum arvense	L.	EQUISETACEAE	field horsetail
Equisetum fluviatile	L.	EQUISETACEAE	water horsetail
Equisetum palustre	L.	EQUISETACEAE	marsh horsetail
Erica tetralix	L.	ERICACEAE	cross-leaved heath
Eriophorum angustifolium	Honck	CYPERACEAE	cotton grass
Euphrasia nemorosa	(Pers.) Wallr.	SCROPHULARIACEAE	eyebright
Fagus sylvatica	L.	FAGACEAE	beech
Fallopia convolvulus	(L.) Á. Löve	POLYGONACEAE	black bindweed
Fallopia japonica (Reynoutria japonica)	(Houtt.) Ronse Decr.	POLYGONACEAE	Japanese knotgrass
Festuca ovina	L.	POACEAE	sheep's fescue
Festuca rubra	L.	POACEAE	red fescue
Festuca vivipara	(L.) Sm.	POACEAE	viviparous fescue
Filipendula ulmaria	(L.) Maxim.	ROSACEAE	meadowsweet
Fragaria vesca	L.	ROSACEAE	wild strawberry
Fraxinus excelsior	L.	OLEACEAE	ash
Galeopsis bifida	Boenn.	LAMIACEAE	bifid hemp nettle
Galeopsis tetrahit	L.	LAMIACEAE	common hempnettle
Galium aparine	L.	RUBIACEAE	cleavers
Galium palustre	L.	RUBIACEAE	marsh bedstraw
Galium saxatile	L.	RUBIACEAE	heath bedstraw
Galium uliginosum	L.	RUBIACEAE	fen bedstraw
Galium verum	L.	RUBIACEAE	lady's bedstraw
Geranium nodosum	L.	GERANIACEAE	knotted crane's bill
Geranium pratense	L.	GERANIACEAE	meadow crane's bill
Geranium sylvaticum	L.	GERANIACEAE	wood crane's bill
Geum rivale	L.	ROSACEAE	water avens
Geum urbanum	L.	ROSACEAE	wood avens

species	authority	family	common name
Glyceria maxima	(Hartm.) Holmb.	POACEAE	reed sweet-grass
Hedera helix	L.	ARALIACEAE	ivy
Heracleum sphondylium	L.	APIACEAE	hogweed
Hesperis matronalis	L.	BRASSICACEAE	dame's violet
Hieracium maculatum (*H. vulgatum*)	Sm.	ASTERACEAE	spotted hawkweed
Hieracium sabaudum	L.	ASTERACEAE	many-leaved hawkweed
Hieracium umbellatum	L.	ASTERACEAE	hawkweed
Holcus lanatus	L.	POACEAE	Yorkshire fog
Holcus mollis	L.	POACEAE	creeping soft grass
Hyacinthoides non-scriptus (*Endymion non-scriptus*)	(L.) Chouard ex Rothm.	LILIACEAE	bluebell
Hypericum perforatum	L.	HYPERACEAE	perforate St John's wort
Hypericum pulchrum	L.	HYPERACEAE	slender St John's wort
Hypochoeris radicata	L.	ASTERACEAE	cat's ear
Iberis amara	L.	BRASSICACEAE	wild candytuft
Impatiens glandulifera	Royle	SCROPHULARIACEAE	Indian balsam
Iris pseudacorus	L.	IRIDACEAE	yellow iris
Juncus acutiflorus	Ehrh. Ex Hoffm.	JUNCACEAE	sharp-flowered rush
Juncus articulatus	L.	JUNCACEAE	jointed rush
Juncus conglomeratus	L.	JUNCACEAE	conglomerate rush
Juncus effusus	L.	JUNCACEAE	soft rush
Knautia arvensis	(L.) Coult.	DIPSACEAE	field scabious
Lamium album	L.	LAMIACEAE	white dead-nettle
Lamium purpureum	L.	LAMIACEAE	red dead-nettle
Lapsana communis	L.	ASTERACEAE	nipplewort
Larix decidua	Mill.	PINACEAE	European larch
Lathyrus pratensis	L.	FABACEAE	meadow vetchling
Leontodon autumnalis	L.	ASTERACEAE	autumn hawkbit
Leontodon hispidus	L.	ASTERACEAE	rough hawkbit
Leucanthemum vulgare (*Chrysanthemum vulgare*)	Lam.	ASTERACEAE	oxeye daisy
Leucojum vernum	L.	AMARYLLIDACEAE	spring snowflake
Ligustrum vulgare	L.	OLEACEAE	wild privet
Linaria vulgaris	Mill.	SCROPHULARIACEAE	common toadflax
Linum catharticum	L.	LINACEAE	fairy flax
Listera ovata	(L.) R.Br.	ORCHIDACEAE	common twayblade
Lolium perenne	L.	POACEAE	perennial rye grass
Lonicera periclymenum	L.	CAPRIFOLIACEAE	honeysuckle
Lotus corniculatus	L.	FABACEAE	bird's-foot trefoil
Lotus pedunculatus (*L. uliginosus*)	Cav.	FABACEAE	large bird's-foot trefoil

species	authority	family	common name
Lupinus arboreus	Sims	FABACEAE	tree lupin
Lupinus nootkatensis	Donn ex Sims	FABACEAE	nootka lupin
Lupinus polyphyllus	Lindl.	FABACEAE	garden lupin
Luzula campestris	(L.) DC.	JUNCACEAE	field woodrush
Luzula sylvatica	(Huds.) Gaudin	JUNCACEAE	greater woodrush
Lycopodium clavatum	L.	LYCOPODIACEAE	stag's horn clubmoss
Lysimachia vulgaris	L.	PRIMULACEAE	yellow loosestrife
Malus domestica	Borkh.	ROSACEAE	apple
Malus sylvestris	(L.) Mill.	ROSACEAE	crab apple
Matricaria discoidea (M. matricarioides)	DC.	ASTERACEAE	pineapple weed
Medicago lupulina	L.	FABACEAE	black medick
Mentha spicata (M. Scotica)	L.	LAMIACEAE	spear mint
Mimulus guttatus	DC.	SCROPHULARIACEAE	monkey flower
Molinia caerulea	(L.) Moench.	POACEAE	purple moor grass
Myosotis arvensis	(L.) Hill	BORAGINACEAE	field forget-me-not
Myosotis scorpoides	L.	BORAGINACEAE	water forget-me-not
Myosotis sylvatica	Hoffm.	BORAGINACEAE	wood forget-me-not
Myrrhis odorata	(L.) Scop.	APIACEAE	sweet cicely
Nardus stricta	L.	POACEAE	mat grass
Odontites vernus	(Bellardi) Dumort.	SCROPHULARIACEAE	red bartsia
Orchis mascula	(L.) L.	ORCHIDACEAE	early purple orchid
Oreopteris limbosperma (Thelypteris limbosperma)	(Bellardi ex All.) Holub	THELYPTERIDACEAE	sweet mountain fern
Papaver dubium	L.	PAPAVARACEAE	long headed poppy
Papaver rhoeus	L.	PAPAVARACEAE	common poppy
Pentaglottis sempervirens	(L.) Tausch ex L.H.Bailey	BORAGINACEAE	green alkanet
Petasites hybridus	(L.) P.Gaertn., B.Mey. & Scherb.	ASTERACEAE	butterbur
Phalaris arundinacea	L.	POACEAE	reed canary-grass
Phleum pratense	L.	POACEAE	timothy
Phragmites communis (P. australis)	Trin.	POACEAE	common reed
Picea sitchensis	(Bong.) Carrière	PINACEAE	sitka spruce

species	authority	family	common name
Pilosella aurantiaca (Hieracium auranticum agg.)	(L.) F.W.Schultz & Sch. Bip.	ASTERACEAE	fox and cubs
Pilosella officinarum (Hieracium pilosella)	F.W.Schultz & Sch. Bip.	ASTERACEAE	mouse-eared hawkweed
Pinus contorta	Douglas ex Louden	PINACEAE	lodgepole pine
Pinus sylvestris	L.	PINACEAE	Scots pine
Plantago lanceolata	L.	PLANTAGINACEAE	ribwort
Plantago major	L.	PLANTAGINACEAE	greater plantain
Plantago media	L.	PLANTAGINACEAE	hoary plantain
Platanthera chlorantha	(Custer) Rchb.	ORCHIDACEAE	great butterfly orchid
Poa annua	L.	POACEAE	annual meadow grass
Poa pratensis	L.	POACEAE	smooth-stalked meadow grass
Poa trivialis	L.	POACEAE	rough meadow grass
Polemonium caeruleum	L.	POLEMONIACEAE	Jacob's ladder
Polygonum aviculare	L.	POLYGONACEAE	knotgrass
Polygonum maculosa (P. persicaria)	Gray	POLYGONACEAE	redshank
Polytrichum commune		BRYOPHYTA	
Polytrichum juniperum		BRYOPHYTA	
Populus tremula	L.	SALICACEAE	aspen
Potamogeton polygonifolius	Pourr.	POTAMOGETONACEAE	bog pondweed
Potentilla anserina	L.	ROSACEAE	silverweed
Potentilla erecta	(L.) Raeusch.	ROSACEAE	tormentil
Potentilla palustris	(L.) Scop.	ROSACEAE	marsh cinquefoil
Potentilla reptans	L.	ROSACEAE	creeping cinquefoil
Primula veris	L.	PRIMULACEAE	cowslip
Primula vulgaris	Huds.	PRIMULACEAE	primrose
Prunella vulgaris	L.	LAMIACEAE	selfheal
Prunus avium	(L.) L.	ROSACEAE	gean (wild cherry)
Prunus spinosa	L.	ROSACEAE	blackthorn
Pteridium aquilinum	(L.) Kuhn	HYPOLEPIDACEAE	bracken
Quercus petraea	(Matt.) Liebl	FAGACEAE	sessile oak
Quercus robur	L.	FAGACEAE	pedunculate oak
Ranunculus acris	L.	RANUNCULACEAE	meadow buttercup
Ranunculus ficaria	L.	RANUNCULACEAE	lesser celandine
Ranunculus repens	L.	RANUNCULACEAE	creeping buttercup
Reseda lutea	L.	RESEDACEAE	wild mignonette
Reseda luteola	L.	RESEDACEAE	weld
Rhinanthus minor	L.	SCROPHULARIACEAE	yellow rattle
Rhytidiadelphus squarrosus		BRYOPHYTA	
Ribes uva-crispa	L.	GROSSULARIACEAE	gooseberry

species	authority	family	common name
Rorippa nasturtium-aquaticum	(L.) Hayek	BRASSICACEAE	water cress
Rosa canina agg.	L.	ROSACEAE	dog rose
Rubus fruticosus agg.	L.	ROSACEAE	bramble (blackberry)
Rubus idaeus	L.	ROSACEAE	raspberry
Rumex acetosa	L.	POLYGONACEAE	common sorrel
Rumex acetosella	L.	POLYGONACEAE	sheep's sorrel
Rumex crispus	L.	POLYGONACEAE	curled dock
Rumex obtusifolius	L.	POLYGONACEAE	broad-leaved dock
Rumex sanguineus	L.	POLYGONACEAE	wood dock
Sagina nodosa	(L.) Fenzl	CARYOPHYLLACEAE	knotted pearlwort
Salix alba	L.	SALICACEAE	white willow
Salix aurita	L.	SALICACEAE	eared willow
Salix caprea	L.	SALICACEAE	goat willow
Salix fragilis	L.	SALICACEAE	crack willow
Salix viminalis	L.	SALICACEAE	osier
Salvia verticillata	L.	LAMIACEAE	whorled clary
Sambucus nigra	L.	CAPRIFOLIACEAE	elder
Scrophularia nodosa	L.	SCROPHULARIACEAE	figwort
Sedum album	L.	CRASSULACEAE	stonecrop
Senecio aquaticus	Hill	ASTERACEAE	marsh ragwort
Senecio jacobaea	L.	ASTERACEAE	common ragwort
Senecio sylvaticus	L.	ASTERACEAE	wood groundsel
Senecio viscosus	L.	ASTERACEAE	sticky groundsel
Senecio vulgaris	L.	ASTERACEAE	groundsel
Silene dioica	(L.) Clairv.	CARYOPHYLLACEAE	red campion
Silene latifolia (S. alba)	Poir.	CARYOPHYLLACEAE	white campion
Silene vulgaris	Garcke	CARYOPHYLLACEAE	bladder campion
Sinapis arvesis	L.	BRASSICACEAE	charlock
Sium latifolium	L.	APIACEAE	water parsnip
Solanum dulcamara	L.	SOLANACEAE	bittersweet
Solidago canadensis	L.	ASTERACEAE	tall goldenrod
Sonchus arvensis	L.	ASTERACEAE	perennial sow-thistle
Sonchus asper	(L.) Hill	ASTERACEAE	prickly sow-thistle
Sorbus aria	(L.) Crantz	ROSACEAE	whitebeam
Sorbus aucuparia	L.	ROSACEAE	rowan (mountain ash)
Sparganium emersum	Rehmann	SPARGANIACEAE	unbranched bur-reed
Sphagnum sp.		BRYOPHYTA	Sphagnum sp.
Stachys palustris	L.	LAMIACEAE	marsh woundwort
Stachys sylvatica	L.	LAMIACEAE	hedge woundwort
Stellaria graminea	L.	CARYOPHYLLACEAE	lesser stitchwort
Stellaria holostea	L.	CARYOPHYLLACEAE	greater stitchwort

species	authority	family	common name
Stellaria media	(L.) Vill.	CARYOPHYLLACEAE	chickweed
Succisa pratensis	Moench	DIPSACEAE	devil's bit scabious
Symphoricarpos albus	(L.)	CAPRIFOLIACEAE	snowberry
Symphytum officinale	L.	BORAGINACEAE	common comfrey
Symphytum x uplandicum	Nyman	BORAGINACEAE	Russian comfrey
Tanacetum parthenium	(L.) Sch. Bip.	ASTERACEAE	feverfew
Tanacetum vulgare	L.	ASTERACEAE	tansy
Taraxacum officinale agg.	Wigg.	ASTERACEAE	dandelion
Teucrium scorodonia	L.	LAMIACEAE	wood sage
Thlaspi arvense	L.	BRASSICACEAE	field penny cress
Torilis japonica	(Houtt.) DC.	APIACEAE	upright hedge parsley
Tragopogon pratensis	L.	ASTERACEAE	goat's-beard
Trifolium campestre	Schreb.	FABACEAE	hop trefoil
Trifolium dubium	Sibth.	FABACEAE	lesser trefoil
Trifolium medium	L.	FABACEAE	zig-zag clover
Trifolium pratense	L.	FABACEAE	red clover
Trifolium repens	L.	FABACEAE	white clover
Tripleurospermum inodorum	(L.) Sch. Bip.	ASTERACEAE	scentless mayweed
Tussilago farfara	L.	ASTERACEAE	coltsfoot
Typha latifolia	L.	TYPHACEAE	bullrush
Ulex europaeus	L.	FABACEAE	gorse (whin, furze)
Ulmus glabra	Huds.	ULMACEAE	wych elm
Urtica dioica	L.	URTICACEAE	stinging nettle
Vaccinium myrtillus	L.	ERICACEAE	blaeberry
Valeriana officinalis	L.	VALARIANACEAE	common valerian
Verbascum thapsus	L.	SCROPHULARIACEAE	great mullein
Veronica arvensis	L.	SCROPHULARIACEAE	wall speedwell
Veronica chamaedrys	L.	SCROPHULARIACEAE	germander speedwell
Veronica officinalis	L.	SCROPHULARIACEAE	heath speedwell
Vicia cracca	L.	FABACEAE	tufted vetch
Vicia hirsuta	(L.) Gray	FABACEAE	tare
Vicia lutea	L.	FABACEAE	yellow vetch
Vicia sepium	L.	FABACEAE	bush vetch

Appendix 3 Autecological keys

Complete keys to the autecological habits presented in Chapter Three (Tables 3.1; 3.6; 3.8) adapted from Hodgson et al, *(1995).*

HABITAT KEY: (terminal habitat in which the species is most frequent)

WOODl = woodland on limestone strata

WASTEl = wasteland on limestone strata

MEADOW = meadows

PASTl = pasture on limestone strata

PASTe = enclosed pasture

QRYl = limestone quarry spoil

RD/RLY = road verges/railway banks

CINDER = cinder tips

HEDGE = hedgerows

COAL = coal mine spoil

SOIL = soil heaps

SCRUB = scrub

SCREE = limestone scree

MIREu = unshaded mire

MIREs = shaded mire.

AGENCY OF DISPERSAL KEY:

WINDp = wind dispersed, dispersule plumed or wrapped in hairs

WINDw = seeds winged or flattened

ANIMa = animal dispersed, dispersule with awn

ANIMm = animal dispersed, dispersule adhesive from mucilage

ANIMi = dispersed, ingested berry

ANIMe = animal dispersed, seed dispersed by ants

UNSP = unspecialised

UNSPag = unspecialised but dispersed widely as a result of agricultural practices

AQ/AN = dipersed by water or animals

AQUAT = dipersed by water.

Appendix 4 Species recorded at Five Sisters

The 52 species recorded as present on Five Sisters (May 1999) during a 2-hour pilot study of the bing and 12 additional species recorded from Greendykes on the same day. The species names appear in the order they were recorded.

SPECIES FROM FIVE SISTERS

Bellis perennis
Plantago lanceolata
Trifolium repens
Prunella vulgaris
Ranunculus repens
R. acris
Taraxacum officinale
Cerastium fontanum
Senecio jacobea
Cardamine hirsuta
Agrostis canina
Holcus lanatus
Festuca rubra
Dactylus glomerata
Rhytidiadelphus squarrosus
Lophocolea sp.
Bryum sp.
Polytrichum juniperinum
Brachythecium rutabulum
Rhytidiadelphus loreus
Bryum capillare
Cladonia fimbriata
Cladonia clorophaea
Atrichum undulatum
Cirsium arvensis
C. vulgare
Sagina sp.
Epilobium spp. x 2
Myosotis sp.
Urtica dioica
Rosa sp.
Sinapis sp.
Rumex acetosa
Tussilago farfara
Reseda luteola
Pseudoscleropodium purum
Poa pratensis
Lolium perenne
Poa annua
Vicia sp.
Hypochoeris radicata
Senecio vulgaris
Equisetum sp.
Stellaria media
Crataegus monogyna
Hieracium pilosella
Rhinanthus minor
Linum catharticum
Euphrasia sp.
Leucanthemum vulgare
Calliergon cuspidatum

SPECIES FROM GREENDYKES

Fragaria vesca
Fraxinus excelsior
Alliaria petiolata
Chamerion angustifolium
Centaurea nigra
Anthriscus sylvestris
Heracleum sphondylium
Rhytidiadelphus triquetrus
Hylocomium splendens
Peltigera canina
Cladonia furcata
Mnium hornum

Appendix 5 Field data recording sheet

Site name:		1	2	3	4	5	6	7	8	9	10
Date: Aspect:											
P / T / M/ B / E Slope:											
Species name		percentage cover per quadrat									
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Notes:											

Appendix 6 Species list from baseline survey

Species name, authority, family and common name are listed for the 211 species recorded in the baseline survey of this study. Alternative species names have been included where these are in common use. Species in bold also appear in the combined species list from other studies (Appendix 2)

species	authority	family	common name
Acer pseudoplatanus	L.	ACERACEAE	sycamore
Achillea millefolium	L.	ASTERACEAE	yarrow
Agrostis gigantea	Roth	POACEAE	black bent
Agrostis stolonifera	L.	POACEAE	brown bent
Agrostis tenuis *(A. capillaris)*	Sibth.	POACEAE	common bent
Alchemilla filicaulis	Buser	ROSACEAE	lady's mantle
Alliaria petiolata	(Bieb.) Cavara & Grande	BRASSICACEAE	garlic mustard
Alnus glutinosa	(L.) Gaertn.	BETULACEAE	alder
Aneura pinguis *(Riccardia pinguis)*	(L.) Dum.	ANEURACEAE	liverwort
Angelica sylvestris	L.	APIACEAE	wild angelica
Anthoxanthum odoratum	L.	POACEAE	sweet vernal grass
Anthriscus sylvestris	(L.) Hoffm.	APIACEAE	cow parsley
Anthyllis vulneraria	L.	FABACEAE	kidney vetch
Arctium minus	(Hill) Bernh.	ASTERACEAE	lesser burdock
Arenaria serpyllifolia	L.	CARYOPHYLLACEAE	thyme leaved sandwort
Arrhenatherum elatius	(L.) Beauv. ex J. & C. Presl	POACEAE	false oat grass
Artemisia absinthium	L.	ASTERACEAE	wormwood
Artemisia vulgaris	L.	ASTERACEAE	mugwort
Barbula recurvirostra	(Hedw.) Dix.	POTTIACEAE	moss
Bellis perennis	L.	ASTERACEAE	daisy
Betula pendula	Roth.	BETULACEAE	silver birch
Betula pubescens	Ehrh.	BETULACEAE	downy birch
Brassica napus	L.	BRASSICACEAE	rape
Bromus ramosus	Huds.	POACEAE	hairy brome
Bryum caespiticium	Hedw.	BRYACEAE	moss
Bryum capillare	Hedw.	BRYACEAE	moss
Bryum pallens	Sw.	BRYACEAE	moss
Calluna vulgaris	(L.) Hull	ERICACEAE	heather, ling
Calystegia sepium	(L.) R. Br.	CONVOLVULACEAE	hedge bindweed
Campanula latifolia	L.	CAMPANULACEAE	giant bellflower
Campylopus atrovirens	De Not.	DICRANACEAE	moss
Campylopus introflexus	(Hedw.) Brid.	DICRANACEAE	moss
Capsella bursa-pastoris	(L.) Medik.	BRASSICACEAE	shepherd's purse
Cardamine hirsuta	L.	BRASSICACEAE	hairy bittercress
Carex flacca	Schreber	CYPERACEAE	carnation grass
Carex nigra	(L.) Reichard	CYPERACEAE	common sedge
Centaurea nigra	L.	ASTERACEAE	black knapweed
Cerastium fontanum	Baumg.	CARYOPHYLLACEAE	common mouse-ear

species	authority	family	common name
Cerastium glomeratum	Thuill.	CARYOPHYLLACEAE	sticky mouse-ear
Chaenorhinum minus	(L.) Lange	SCROPHULARIACEAE	small toadflax
Chamerion angustifolium	(L.) Holub	ONAGRACEAE	rosebay willowherb
Chenopodium album	L.	CHENOPODIACEAE	fat hen
Cirriphyllum crassinervium	(Tayl.) Loeske	BRACHYTHECIACEAE	moss
Cirsium arvense	(L.) Scop.	ASTERACEAE	creeping thistle
Cirsium palustre	(L.) Scop.	ASTERACEAE	marsh thistle
Cirsium vulgare	(Sari) Ten.	ASTERACEAE	spear thistle
Cladonia fimbriata	(L.) Fr.	CLADONIACEAE	lichen
Cladonia squamosa	(Scop.) Hoffm.	CLADONIACEAE	lichen
Conopodium majus	(Gouan) Loret	APIACEAE	pignut
Corylus avellana	L.	CORYLACEAE	hazel
Crataegus monogyna	Jacq.	ROSACEAE	hawthorn
Cymbalaria muralis	P.Gaertner, B.Meyer & Scherb.	SCROPHULARIACEAE	ivy-leaved toadflax
Cynosurus cristatus	L.	POACEAE	crested dog's tail
Cytisus scoparius	(L.) Link.	FABACEAE	broom
Dactylis glomerata	L.	POACEAE	cocksfoot
Dactylorhiza fuchsii	Druce	ORCHIDACEAE	common spotted orchid
Deschampsia cespitosa	(L.) Beauv.	POACEAE	tufted hair grass
Deschampsia flexuosa	(L.) Trin.	POACEAE	wavy hair grass
Dicranella heteromalla	(Hedw.) Schimp.	DICRANACEAE	moss
Dicranum scoparium	Hedw.	DICRANACEAE	moss
Digitalis purpurea	L.	SCROPHULARIACEAE	foxglove
Diploicia canescens	(Dickson) Massal.	PHYSCIACEAE	lichen
Dryopteris dilitata	(Hoffm.) A.Gray	ASPIDACEAE	common buckler fern
Dryopteris filix-mas	(L.) Schott	ASPIDACEAE	male fern
Epilobium hirsutum	L.	ONAGRACEAE	great willowherb
Epilobium montanum	L.	ONAGRACEAE	broad-leaved willowherb
Epilobium palustre	L.	ONAGRACEAE	marsh willowherb
Equisetum arvense	L.	EQUISETACEAE	field horsetail
Equisetum sylvaticum	L.	EQUISETACEAE	wood horsetail
Erica cinerea	L.	ERICACEAE	bell heather
Euphrasia nemorosa	(Pers.) Wallr.	SCROPHULARIACEAE	eyebright
Fagus sylvatica	L.	FAGACEAE	beech
Festuca ovina	L.	POACEAE	sheep's fescue
Filipendula ulmaria	(L.) Maxim.	ROSACEAE	meadowsweet
Fragaria vesca	L.	ROSACEAE	wild strawberry
Fraxinus excelsior	L.	OLEACEAE	ash
Galeopsis tetrahit	L.	LAMIACEAE	common hempnettle
Galium aparine	L.	RUBIACEAE	cleavers
Galium saxatile	L.	RUBIACEAE	heath bedstraw

species	authority	family	common name
Geranium robertianum	L.	GERANIACEAE	herb robert
Geum urbanum	L.	ROSACEAE	wood avens
Grimmia pulvinata	(Hedw.) Sm.	GRIMMIACEAE	moss
Heracleum sphondylium	L.	APIACEAE	hogweed
Hesperis matronalis	L.	BRASSICACEAE	dame's violet
Hieracium sabaudum	L.	ASTERACEAE	many-leaved hawkweed
Hippophae rhamnoides	L.	ELAEAGNACEAE	sea buckthorn
Holcus lanatus	L.	POACEAE	Yorkshire fog
Holcus mollis	L.	POACEAE	creeping soft grass
Hylocomium splendens	(Hedw.) Br. Eur.	HYPNACEAE	moss
Hypericum perforatum	L.	HYPERACEAE	perforate St John's wort
Hypericum pulchrum	L.	HYPERACEAE	slender St John's wort
Hypnum cupressiforme	Hedw.	HYPNACEAE	moss
Hypnum jutlandicum	Holmen & Warncke	HYPNACEAE	moss
Hypnum mammillatum	(Brid.) Loeske	HYPNACEAE	moss
Hypochoeris radicata	L.	ASTERACEAE	cat's ear
Juncus conglomeratus	L.	JUNCACEAE	conglomerate rush
Juncus effusus	L.	JUNCACEAE	soft rush
Knautia arvensis	(L.) Coult.	DIPSACEAE	field scabious
Lamium purpureum	L.	LAMIACEAE	red dead-nettle
Larix decidua	Mill.	PINACEAE	European larch
Larix x eurolepis	Henry	PINACEAE	Dunkeld larch
Lathyrus pratensis	L.	FABACEAE	meadow vetchling
Leucanthemum vulgare *(Chrysanthemum vulgare)*	Lam.	ASTERACEAE	oxeye daisy
Ligustrum vulgare	L.	OLEACEAE	wild privet
Linaria vulgaris	Mill.	SCROPHULARIACEAE	common toadflax
Linum catharticum	L.	LINACEAE	fairy flax
Listera ovata	(L.) R.Br.	ORCHIDACEAE	common twayblade
Lolium perenne	L.	POACEAE	perennial rye grass
Lophocolea bidentata	(L.) Dum.	LOPHOCOLEACEAE	liverwort
Lophocolea cuspidata	(Nees.) Limpr.	LOPHOCOLEACEAE	liverwort
Lotus corniculatus	L.	FABACEAE	bird's-foot trefoil
Lotus pedunculatus *(L. uliginosus)*	Cav.	FABACEAE	large bird's-foot trefoil
Lupinus arboreus	Sims	FABACEAE	tree lupin
Lupinus nootkatensis	Donn ex Sims	FABACEAE	nootka lupin

species	authority	family	common name
Luzula multiflora	(Retz.) Lej.	JUNCACEAE	many-headed woodrush
Lysimachia vulgaris	L.	PRIMULACEAE	yellow loosestrife
Matricaria discoidea *(M. matricarioides)*	DC.	ASTERACEAE	pineapple weed
Medicago lupulina	L.	FABACEAE	black medick
Melilotus altissimus	Thuill.	FABACEAE	tall melilot
Myosotis arvensis	(L.) Hill	BORAGINACEAE	field forget-me-not
Myosotis sylvatica	Hoffm.	BORAGINACEAE	wood forget-me-not
Odontites vernus	(Bellardi) Dumort.	SCROPHULARIACEAE	red bartsia
Oligotrichum hercynicum	(Hedw.) Lam. & Cand.	POLYTRICHACEAE	moss
Papaver dubium	L.	PAPAVARACEAE	long headed poppy
Papaver somniferum	L.	PAPAVARACEAE	opium poppy
Peltigera canina	(L.) Willd.	PELTIGERACEAE	lichen
Pertusaria corallina	(L.) Arnold	PERTUSARIACEAE	lichen
Phleum pratense	L.	POACEAE	timothy
Phragmites communis *(P. australis)*	Trin.	POACEAE	common reed
Picea sitchensis	(Bong.) Carrière	PINACEAE	sitka spruce
Pilosella aurantiaca *(Hieracium aurantiacum agg.)*	(L.) F.W.Schultz & Sch. Bip.	ASTERACEAE	fox and cubs
Pilosella officinarum *(Hieracium pilosella)*	F.W.Schultz & Sch. Bip.	ASTERACEAE	mouse-eared hawkweed
Plantago lanceolata	L.	PLANTAGINACEAE	ribwort
Plantago major	L.	PLANTAGINACEAE	greater plantain
Pleurozium schreberi	(Brid.) Mitt.	HYPNACEAE	moss
Poa annua	L.	POACEAE	annual meadow grass
Poa nemoralis	L.	POACEAE	wood meadow-grass
Poa trivialis	L.	POACEAE	rough meadow grass
Polemonium caeruleum	L.	POLEMONIACEAE	Jacob's ladder
Polygonum aviculare	L.	POLYGONACEAE	knotgrass
Polygonum maculosa *(P. persicaria)*	Gray	POLYGONACEAE	redshank
Polytrichum commune	Hedw.	POLYTRICHACEAE	moss
Polytrichum juniperum	Hedw.	POLYTRICHACEAE	moss
Potentilla anserina	L.	ROSACEAE	silverweed
Potentilla erecta	(L.) Raeusch.	ROSACEAE	tormentil
Pottia truncata	(Hedw.) Fürnr.	POTTIACEAE	moss
Primula veris	L.	PRIMULACEAE	cowslip
Prunella vulgaris	L.	LAMIACEAE	selfheal
Prunus spinosa	L.	ROSACEAE	blackthorn
Pteridium aquilinum	(L.) Kuhn	HYPOLEPIDACEAE	bracken

species	authority	family	common name
Quercus robur	L.	FAGACEAE	pedunculate oak
Racomitrium canescens	(Hedw.) Brid.	GRIMMIACEAE	moss
Ranunculus acris	L.	RANUNCULACEAE	meadow buttercup
Ranunculus repens	L.	RANUNCULACEAE	creeping buttercup
Raphanus raphanistrum	L.	BRASSICACEAE	wild radish
Reseda luteola	L.	RESEDACEAE	weld
Rhinanthus minor	L.	SCROPHULARIACEAE	yellow rattle
Rhytidiadelphus squarrosus	(Hedw.) Warnst.	HYPNACEAE	moss
Rhytidiadelphus triquetrus	(Hedw.) Warnst.	HYPNACEAE	moss
Rosa canina agg.	L.	ROSACEAE	dog rose
Rubus fruticosus agg.	L.	ROSACEAE	bramble (blackberry)
Rubus idaeus	L.	ROSACEAE	raspberry
Rumex acetosa	L.	POLYGONACEAE	common sorrel
Rumex acetosella	L.	POLYGONACEAE	sheep's sorrel
Rumex crispus	L.	POLYGONACEAE	curled dock
Rumex obtusifolius	L.	POLYGONACEAE	broad-leaved dock
Sagina procumbens	L.	CARYOPHYLLACEAE	procumbent pearlwort
Salix caprea	L.	SALICACEAE	goat willow
Sambucus nigra	L.	CAPRIFOLIACEAE	elder
Sanguisorba minor	Scop.	ROSACEAE	salad burnet
Senecio jacobaea	L.	ASTERACEAE	common ragwort
Senecio viscosus	L.	ASTERACEAE	sticky groundsel
Senecio vulgaris	L.	ASTERACEAE	groundsel
Silene dioica	(L.) Clairv.	CARYOPHYLLACEAE	red campion
Silene latifolia *(S. alba)*	Poir.	CARYOPHYLLACEAE	white campion
Silene vulgaris	Garcke	CARYOPHYLLACEAE	bladder campion
Sinapis arvesis	L.	BRASSICACEAE	charlock
Solanum dulcamara	L.	SOLANACEAE	bittersweet
Sonchus asper	(L.) Hill	ASTERACEAE	prickly sow-thistle
Sonchus oleraceus	L.	ASTERACEAE	sow-thistle
Sorbus aucuparia	L.	ROSACEAE	rowan (mountain ash)
Stachys palustris	L.	LAMIACEAE	marsh woundwort
Stellaria graminea	L.	CARYOPHYLLACEAE	lesser stitchwort
Stellaria holostea	L.	CARYOPHYLLACEAE	greater stitchwort
Stellaria media	(L.) Vill.	CARYOPHYLLACEAE	chickweed
Succisa pratensis	Moench	DIPSACEAE	devil's bit scabious
Symphoricarpos albus	(L.)	CAPRIFOLIACEAE	snowberry
Tanacetum parthenium	(L.) Sch. Bip.	ASTERACEAE	feverfew
Tanacetum vulgare	L.	ASTERACEAE	tansy
Taraxacum officinale agg.	Wigg.	ASTERACEAE	dandelion
Thlaspi arvense	L.	BRASSICACEAE	field penny cress
Tragopogon pratensis	L.	ASTERACEAE	goat's-beard

species	authority	family	common name
Trifolium campestre	Schreb.	FABACEAE	hop trefoil
Trifolium hybridum	L.	FABACEAE	alsike clover
Trifolium medium	L.	FABACEAE	zig-zag clover
Trifolium pratense	L.	FABACEAE	red clover
Trifolium repens	L.	FABACEAE	white clover
Tripleurospermum inodorum	(L.) Sch. Bip.	ASTERACEAE	scentless mayweed
Tussilago farfara	L.	ASTERACEAE	coltsfoot
Ulex europaeus	L.	FABACEAE	gorse (whin, furze)
Ulmus glabra	Huds.	ULMACEAE	wych elm
Urtica dioica	L.	URTICACEAE	stinging nettle
Veronica chamaedrys	L.	SCROPHULARIACEAE	germander speedwell
Veronica persica	Poiret	SCROPHULARIACEAE	large field speedwell
Veronica polita	Fries	SCROPHULARIACEAE	grey speedwell
Veronica serpyllifolia	L.	SCROPHULARIACEAE	thyme-leaved speedwell
Viburnum opulus	L.	CAPRIFOLIACEAE	guelder rose
Vicia cracca	L.	FABACEAE	tufted vetch
Vicia hirsuta	(L.) Gray	FABACEAE	tare
Vicia sativa	L.	FABACEAE	common vetch
Viola arvensis	Murray	VIOLACEAE	field violet

Appendix 7 Shannon-Weiner diversity indices and evenness scores

Shannon-Weiner diversity indices and evenness scores,
species are listed for each of the 340 recording quadrats in the baseline survey

Releve	H	J	no of spp.	Releve	H	J	no of spp.
ANB1	4.31	0.77	29	ASB2	2.42	0.45	17
ANB10	2.21	0.40	7	ASB3	3.18	0.59	19
ANB11	2.32	0.42	10	ASB4	3.19	0.60	19
ANB12	2.63	0.47	9	ASB5	2.39	0.45	16
ANB2	2.79	0.50	16	ASB6	3.19	0.60	17
ANB3	2.15	0.39	8	ASB7	2.49	0.46	15
ANB4	2.66	0.48	16	ASB8	1.99	0.37	15
ANB5	2.38	0.43	7	ASB9	2.33	0.44	18
ANB6	2.48	0.44	14	ASE1	2.26	0.46	7
ANB7	2.92	0.52	10	ASE10	2.04	0.41	10
ANB8	3.06	0.55	14	ASE2	2.67	0.54	9
ANB9	3.07	0.55	16	ASE3	3.13	0.63	15
ANM1	3.38	0.59	19	ASE4	3.11	0.63	12
ANM10	2.63	0.46	17	ASE5	3.07	0.62	12
ANM11	2.66	0.47	15	ASE6	1.59	0.32	6
ANM2	1.88	0.33	12	ASE7	2.48	0.50	9
ANM3	2.75	0.48	13	ASE8	2.52	0.51	19
ANM4	4.01	0.70	20	ASE9	2.61	0.53	13
ANM5	2.53	0.44	9	ASM1	2.15	0.38	13
ANM6	2.81	0.49	15	ASM10	2.39	0.42	12
ANM7	1.97	0.35	12	ASM11	2.50	0.44	17
ANM8	2.84	0.50	15	ASM12	2.42	0.43	20
ANM9	1.56	0.27	9	ASM13	2.28	0.40	16
ANT1	2.62	0.47	11	ASM14	2.42	0.43	12
ANT10	2.56	0.46	15	ASM15	2.74	0.48	18
ANT11	3.23	0.58	18	ASM16	2.29	0.40	15
ANT12	3.53	0.64	18	ASM17	2.61	0.46	11
ANT13	3.23	0.59	18	ASM2	2.31	0.41	9
ANT14	3.61	0.65	19	ASM3	2.34	0.41	13
ANT15	3.84	0.69	20	ASM4	2.04	0.36	15
ANT16	2.52	0.46	12	ASM5	2.68	0.47	11
ANT2	2.36	0.43	16	ASM6	1.58	0.28	7
ANT3	3.45	0.63	19	ASM7	2.49	0.44	11
ANT4	1.88	0.34	7	ASM8	2.18	0.39	10
ANT5	3.08	0.56	16	ASM9	2.19	0.39	8
ANT6	2.31	0.42	11	AST1	0.98	0.18	5
ANT7	1.78	0.32	14	AST10	2.58	0.48	15
ANT8	1.81	0.33	11	AST11	2.02	0.38	15
ANT9	1.96	0.36	7	AST12	1.97	0.37	13

Releve	H	J	no of spp.	Releve	H	J	no of spp.
ASB1	2.95	0.55	13	AST13	2.11	0.39	14
ASB10	2.62	0.49	13	AST14	0.79	0.15	6
AST15	1.88	0.35	9	CLM2	3.40	0.60	17
AST16	1.20	0.22	7	CLM20	3.21	0.56	13
AST17	1.30	0.24	5	CLM3	3.24	0.57	16
AST2	1.55	0.29	8	CLM4	3.41	0.60	15
AST3	1.37	0.26	8	CLM5	3.48	0.61	17
AST4	0.75	0.14	3	CLM6	3.25	0.57	13
AST5	1.81	0.34	5	CLM7	3.56	0.62	17
AST6	1.44	0.27	6	CLM8	3.77	0.66	22
AST7	1.13	0.21	7	CLM9	3.76	0.66	19
AST8	1.38	0.26	6	CLT1	3.00	0.57	16
AST9	1.30	0.24	9	CLT10	3.29	0.62	13
CLB1	2.05	0.33	12	CLT11	3.37	0.64	17
CLB10	2.35	0.38	10	CLT2	2.72	0.52	10
CLB11	3.38	0.55	20	CLT3	4.12	0.78	16
CLB12	3.30	0.53	17	CLT4	3.09	0.58	14
CLB13	3.51	0.57	17	CLT5	3.72	0.70	18
CLB14	2.54	0.41	13	CLT6	3.01	0.57	11
CLB15	3.04	0.49	13	CLT7	2.55	0.48	8
CLB16	3.01	0.49	15	CLT8	4.17	0.79	18
CLB17	2.89	0.47	16	CLT9	3.19	0.60	14
CLB18	3.01	0.49	16	DNB1	2.99	0.59	19
CLB19	1.96	0.32	8	DNB10	2.16	0.43	7
CLB2	2.54	0.41	16	DNB2	2.89	0.57	13
CLB20	2.74	0.44	9	DNB3	2.37	0.47	17
CLB21	2.89	0.47	12	DNB4	3.08	0.61	18
CLB22	3.37	0.55	10	DNB5	3.72	0.74	23
CLB3	2.82	0.46	14	DNB6	2.41	0.48	16
CLB4	3.30	0.53	17	DNB7	2.89	0.57	11
CLB5	1.00	0.16	10	DNB8	2.82	0.56	8
CLB6	2.96	0.48	14	DNB9	3.49	0.69	16
CLB7	3.21	0.52	15	DNM1	2.34	0.48	8
CLB8	3.75	0.61	18	DNM10	2.99	0.62	15
CLB9	2.98	0.48	11	DNM2	2.51	0.52	10
CLM1	3.79	0.66	18	DNM3	2.49	0.51	11
CLM10	2.79	0.49	12	DNM4	2.46	0.51	12
CLM11	3.23	0.57	14	DNM5	2.77	0.57	11
CLM12	2.85	0.50	13	DNM6	3.02	0.62	15
CLM13	3.15	0.55	17	DNM7	2.83	0.58	11
CLM14	3.33	0.59	16	DNM8	2.98	0.61	14
CLM15	2.88	0.51	11	DNM9	2.85	0.59	11
CLM16	2.79	0.49	12	DNP1	2.79	0.67	9

Releve	H	J	no of spp.	Releve	H	J	no of spp.
CLM17	3.36	0.59	14	DNP10	2.76	0.66	10
CLM18	2.97	0.52	11	DNP2	2.67	0.64	10
CLM19	3.09	0.54	13	DNP3	2.98	0.72	13
DNP4	2.10	0.50	6	GDB25	1.72	0.30	12
DNP5	2.40	0.58	8	GDB3	2.37	0.42	14
DNP6	1.91	0.46	5	GDB4	2.10	0.37	14
DNP7	2.82	0.68	8	GDB5	2.66	0.47	21
DNP8	1.72	0.41	5	GDB6	2.39	0.42	12
DNP9	2.36	0.57	7	GDB7	2.11	0.37	10
DNT1	1.95	0.48	9	GDB8	2.49	0.44	12
DNT10	2.36	0.58	6	GDB9	2.77	0.49	14
DNT2	2.51	0.62	9	GDP1	3.28	0.29	17
DNT3	1.15	0.28	4	GDP10	2.14	0.19	9
DNT4	1.45	0.36	4	GDP11	3.11	0.27	18
DNT5	0.86	0.21	5	GDP12	3.35	0.29	15
DNT6	2.23	0.55	7	GDP13	2.22	0.19	12
DNT7	2.60	0.64	10	GDP14	3.01	0.26	14
DNT8	2.02	0.50	8	GDP15	3.42	0.30	16
DNT9	2.17	0.53	8	GDP16	3.29	0.29	19
DSB1	2.34	0.43	13	GDP17	2.72	0.24	10
DSB10	3.25	0.60	16	GDP18	2.87	0.25	15
DSB11	3.08	0.56	16	GDP19	3.08	0.27	16
DSB2	2.80	0.51	15	GDP2	3.20	0.28	20
DSB3	3.04	0.56	13	GDP20	2.94	0.26	15
DSB4	3.16	0.58	19	GDP3	3.19	0.28	17
DSB5	2.46	0.45	13	GDP4	3.60	0.32	25
DSB6	2.25	0.41	13	GDP5	3.30	0.29	19
DSB7	2.53	0.46	15	GDP6	2.88	0.25	13
DSB8	2.85	0.52	13	GDP7	3.05	0.27	14
DSB9	3.01	0.55	16	GDP8	2.76	0.24	16
GDB1	3.50	0.62	18	GDP9	2.13	0.19	12
GDB10	2.03	0.36	8	GDT1	2.51	0.49	7
GDB11	2.70	0.48	15	GDT10	2.00	0.39	10
GDB12	2.39	0.42	8	GDT11	2.25	0.43	11
GDB13	2.23	0.40	7	GDT12	1.77	0.34	9
GDB14	1.76	0.31	8	GDT13	2.51	0.49	8
GDB15	2.11	0.37	7	GDT14	1.59	0.31	3
GDB16	1.63	0.29	4	GDT15	2.45	0.47	8
GDB17	0.00	0.00	0	GDT16	2.39	0.46	8
GDB18	2.16	0.38	6	GDT17	2.36	0.46	8
GDB19	0.50	0.09	2	GDT18	1.86	0.36	7
GDB2	3.55	0.63	24	GDT19	2.81	0.54	7
GDB20	1.15	0.20	3	GDT2	2.73	0.53	9

Releve	H	J	no of spp.	Releve	H	J	no of spp.
GDB21	1.45	0.26	6	GDT20	1.55	0.30	4
GDB22	1.96	0.35	14	GDT21	2.32	0.45	8
GDB23	1.16	0.21	7	GDT22	1.00	0.19	5
GDB24	2.23	0.40	13	GDT23	2.51	0.49	11
GDT24	2.23	0.43	7	MBT1	2.58	0.75	10
GDT25	1.56	0.30	14	MBT2	1.88	0.12	6
GDT3	2.44	0.47	11	MBT3	1.15	0.33	3
GDT4	2.81	0.54	14	MBT4	2.32	0.67	9
GDT5	3.08	0.60	11	MBT5	1.72	0.50	13
GDT6	2.35	0.46	10	OBB1	3.11	0.56	16
GDT7	1.03	0.20	9	OBB10	2.68	0.48	13
GDT8	0.92	0.18	2	OBB2	2.75	0.49	16
GDT9	1.09	0.21	3	OBB3	1.75	0.31	10
MBB1	2.64	0.46	17	OBB4	1.68	0.30	9
MBB10	2.94	0.51	16	OBB5	2.00	0.36	9
MBB11	1.94	0.33	13	OBB6	2.55	0.46	10
MBB12	0.76	0.13	5	OBB7	2.21	0.40	18
MBB13	3.58	0.62	20	OBB8	2.33	0.42	13
MBB14	3.19	0.55	15	OBB9	2.25	0.40	14
MBB15	3.38	0.58	19	OBM1	2.85	0.52	19
MBB2	1.20	0.21	4	OBM10	1.94	0.35	14
MBB3	2.62	0.45	9	OBM2	2.93	0.53	17
MBB4	2.61	0.45	14	OBM3	2.40	0.44	11
MBB5	2.00	0.34	9	OBM4	2.12	0.39	11
MBB6	2.24	0.39	7	OBM5	2.56	0.47	17
MBB7	2.29	0.39	19	OBM6	1.60	0.29	10
MBB8	3.09	0.53	18	OBM7	2.08	0.38	9
MBB9	2.86	0.49	18	OBM8	3.13	0.57	23
MBE1	1.79	0.35	12	OBM9	2.99	0.54	19
MBE10	2.84	0.55	15	OBT1	2.89	0.54	14
MBE2	2.12	0.41	13	OBT10	3.12	0.58	16
MBE3	2.84	0.55	17	OBT11	3.12	0.58	18
MBE4	2.69	0.52	12	OBT12	2.03	0.38	13
MBE5	3.24	0.63	22	OBT13	2.95	0.55	17
MBE6	2.78	0.54	16	OBT2	2.65	0.50	14
MBE7	2.51	0.49	12	OBT3	2.27	0.42	14
MBE8	1.68	0.33	12	OBT4	2.79	0.52	15
MBE9	2.75	0.53	11	OBT5	2.79	0.52	14
MBM1	3.75	0.70	25	OBT6	2.98	0.56	18
MBM10	1.47	0.28	10	OBT7	3.16	0.59	17
MBM2	2.16	0.41	14	OBT8	2.90	0.54	11
MBM3	3.17	0.60	9	OBT9	3.41	0.64	20

Releve	H	J	no of spp.
MBM4	2.42	0.45	7
MBM5	2.67	0.50	10
MBM6	3.36	0.63	16
MBM7	1.78	0.34	8
MBM8	0.53	0.10	3
MBM9	2.27	0.43	11

Appendix 8 C-S-R Functional Type

The species recorded in the baseline survey are listed by C-S-R functional type as allocated by Hodgson et al. (1999)

species name	functional type	species name	functional type
Chamerion angustifolium	c	*Carex flacca*	s
Cirsium arvense	c	*Festuca ovina*	s
Epilobium hirsutum	c	*Galium saxatile*	s
Fraxinus excelsior	c	*Hypericum pulchrum*	s
Phragmites australis	c	*Luzula multiflora*	s
Pteridium aquilinum	c	*Sanguisorba minor*	s
Sambucus nigra	c	*Succisa pratensis*	s
Ulmus glabra	c		
Urtica dioica	c	*Anthyllis vulneraria*	s/sr
Angelica sylvestris	c/cr	*Carex nigra*	s/sc
Artemesia vulgaris	c/cr	*Deschampsia flexuosa*	s/sc
Calystegia sepium	c/cr	*Erica cinerea*	s/sc
Tanacetum vulgare	c/cr		
		Dactylorhiza fuchsii	s/csr
Acer pseudoplatanus	c/sc	*Epilobium palustre*	s/csr
Betula pendula	c/sc	*Geum urbanum*	s/csr
Betula pubescens	c/sc	*Listera ovata*	s/csr
Filipendula ulmaria	c/sc	*Lotus corniculatus*	s/csr
Juncus conglomeratus	c/sc	*Pilosella officinarum*	s/csr
Juncus effusus	c/sc	*Poa nemoralis*	s/csr
Lysimachia vulgaris	c/sc	*Potentilla erecta*	s/csr
		Primula veris	s/csr
Arrhenatherum elatius	c/csr		
Dactylis glomerata	c/csr	*Alnus glutinosa*	sc
Holcus mollis	c/csr	*Calluna vulgaris*	sc
Leucanthemum vulgare	c/csr	*Corylus avellana*	sc
Lotus pedunculatus	c/csr	*Crataegus monogyna*	sc
Solanum dulcamara	c/csr	*Cytisus scoparius*	sc
Vicia cracca	c/csr	*Fagus sylvatica*	sc
		Ligustrum vulgare	sc
Agrostis gigantea	cr	*Prunus spinosa*	sc
Agrostis stolonifera	cr	*Quercus robur*	sc
Alliaria petiolata	cr	*Rosa canina*	sc
Anthriscus sylvestris	cr	*Rubus fruticosus*	sc
Arctium minus	cr	*Rubus idaeus*	sc
Cirsium palustre	cr	*Sorbus aucuparia*	sc
Cirsium vulgare	cr	*Ulex europaeus*	sc
Equisetum arvense	cr	*Viburnum opulus*	sc
Galium aparine	cr		
Heracleum sphondylium	cr	*Arenaria serpyllifolia*	sr
Linaria vulgaris	cr	*Cardamine hirsuta*	sr
Ranunculus repens	cr	*Conopodium majus*	sr
Rumex obtusifolius	cr	*Euphrasia nemorosa*	sr
Stachys palustris	cr	*Linum catharticum*	sr
Tussilago farfara	cr	*Trifolium campestre*	sr

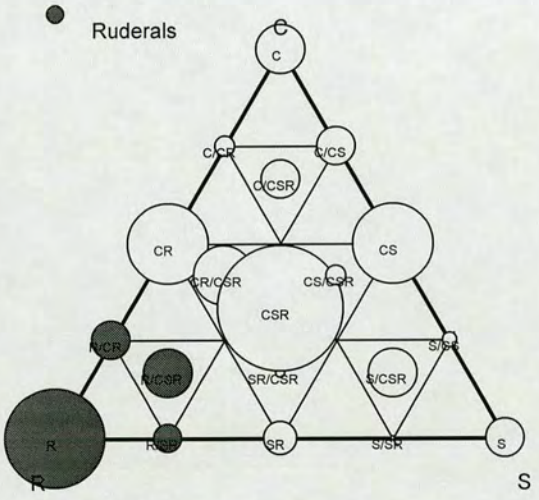
species name	functional type	species name	functional type
Capsella bursa-patoris	r	*Agrostis tenuis*	csr
Lamium purpureum	r	*Bromus ramosus*	csr
Matricaria discoidea	r	*Centaurea nigra*	csr
Odontites vernus	r	*Cymbalaria muralis*	csr
Papavar dubium	r	*Cynosurus cristatus*	csr
Persicaria maculosa	r	*Epilobium montanum*	csr
Poa annua	r	*Fragaria vesca*	csr
Polygonum aviculare	r	*Holcus lanatus*	csr
Raphanus raphanistrum	r	*Hypochaeris radicata*	csr
Senecio viscosus	r	*Knautia arvensis*	csr
Senecio vulgaris	r	*Lathyrus pratensis*	csr
Sinapsis arvensis	r	*Phleum pratense*	csr
Stellaria media	r	*Plantago lanceolata*	csr
Thlaspi arvense	r	*Prunella vulgaris*	csr
Tripleurospermum inodorum	r	*Ranunculus acris*	csr
Veronica persica	r	*Rumex acetosa*	csr
Veronica polita	r	*Silene latifolia*	csr
Viola arvensis	r	*Silene vulgaris*	csr
		Stellaria graminea	csr
Cerastium glomeratum	r/sr	*Stellaria holostea*	csr
Chaenorhinum minus	r/sr	*Trifolium hybridum*	csr
Medicago lupulina	r/sr	*Trifolium pratense*	csr
Myosotis arvensis	r/sr	*Veronica chamaedrys*	csr
Rhinanthus minor	r/sr		
		Achillea millefolium	cr/csr
Alchemilla filicaulis	r/cr	*Artemesia absinthium*	cr/csr
Chenopodium album	r/cr	*Digitalis purpureum*	cr/csr
Fallopia convolvulus	r/cr	*Hesperis matronalis*	cr/csr
Galeopsis tetrahit	r/cr	*Hypericum perforatum*	cr/csr
Rumex crispus	r/cr	*Lolium perenne*	cr/csr
Senecio jacobaea	r/cr	*Poa trivialis*	cr/csr
Silene dioica	r/cr	*Potentilla anserina*	cr/csr
Sonchus asper	r/cr	*Tanacetum parthenium*	cr/csr
Sonchus oleraceus	r/cr	*Tragopogon pratensis*	cr/csr
		Trifolium repens	cr/csr
Bellis perennis	r/csr		
Cerastium fontanum	r/csr	*Deschampsia cespitosa*	sc/csr
Geranium robertianum	r/csr	*Dryopteris dilatata*	sc/csr
Plantago major	r/csr	*Dryopteris filix-mas*	sc/csr
Reseda luteola	r/csr	*Trifolium medium*	sc/csr
Sagina procumbens	r/csr		
Taraxacum officinale	r/csr	*Anthoxanthum odoratum*	sr/csr
Veronica serpyllifolia	r/csr	*Rumex acetosella*	sr/csr
Vicia hirsutum	r/csr		
Vicia sativa	r/csr		

Remaining 50 species that have not been allocated to any C-S-R functional type	
Barbula recurvostra	*Lophocoela cuspidata*
Brassica napus	*Lophocoelea bidenta*
Bryum caespiticium	*Lupinus arboreus*
Bryum capillare	*Lupinus nootkatensis*
Bryum pallens	*Melilotus altissimus*
Campanula latifolia	*Myosotis sylvatica*
Campylopus atrovirens	*Oligitrichum hercynicum*
Campylopus introflexus	*Papavar somniferum*
Cirriphyllum crassinervum	*Peltigra canina*
Cladonia fimbriata	*Pertusaria corallina*
Cladonia squamosa	*Picea sitchensis*
Dicranella heteromalla	*Pillosella aurantiaca*
Dicranium commune	*Pleurozium schreberi*
Dicranium scoparium	*Polemonium caeruleum*
Diploica canescens	*Polytrichum commune*
Equisetum sylvaticum	*Polytrichum juniperis*
Grimmia pulvinata	*Pottia davalliana*
Hieracium auraticeum	*Pottia truncata*
Hieracium sabaudum	*Racomitrium canescens*
Hieracium strictiforme	*Rhytidiadelphus squarrosis*
Hippophae rhamnoides	*Rhytidiadelphus triquestris*
Hylocomium splendens	*Riccardia pinguis*
Hypnum cupressiforme	*Salix caprea*
Hypnum filliforme	*Symphoricarpos albus*
Hypnum jutlandica	
Hypnum lacunosum	
Larix decidua	
Larix x marschlinsii	

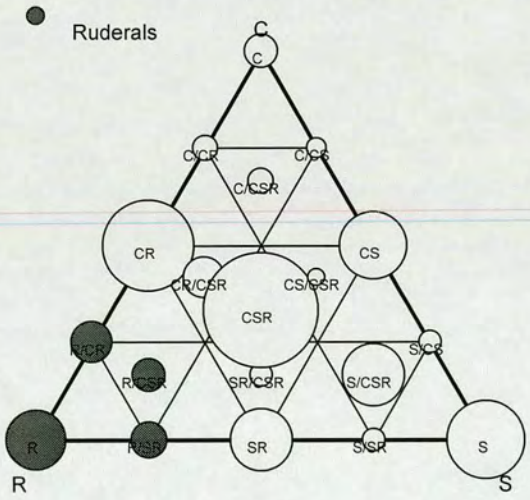
Appendix 9 Ternary bubble plots

Ternary bubble plots of the signatures points of the baseline data (a) and the British 500 data (b) that were presented in Chapter Three figure 3.9 demonstrating that more bing species are allocated to ruderal strategies than would be expected from the allocation of common British species. Bubble plots of selected positions on site exemplify areas within the bings where most species are allocated to one strategy: (c) Clapperton top quadrats – CLT – ruderal strategy; (d) Drumshoreland north top quadrats – DNT – competitive strategy; (e) Mid Breich top quadrats – MBT – stress tolerant strategy; (f) Oakbank top quadrats – OBT – intermediate CSR strategy

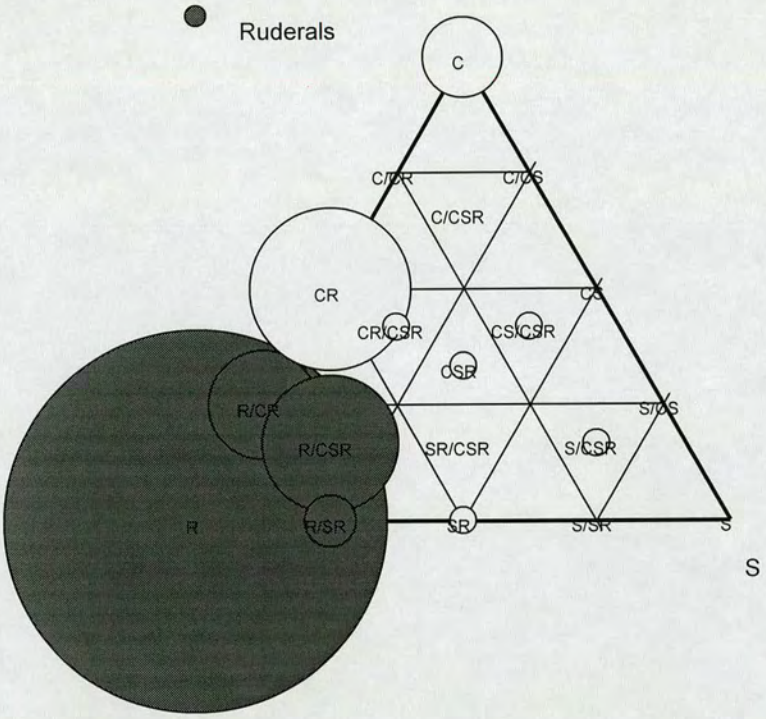
(a) Baseline data



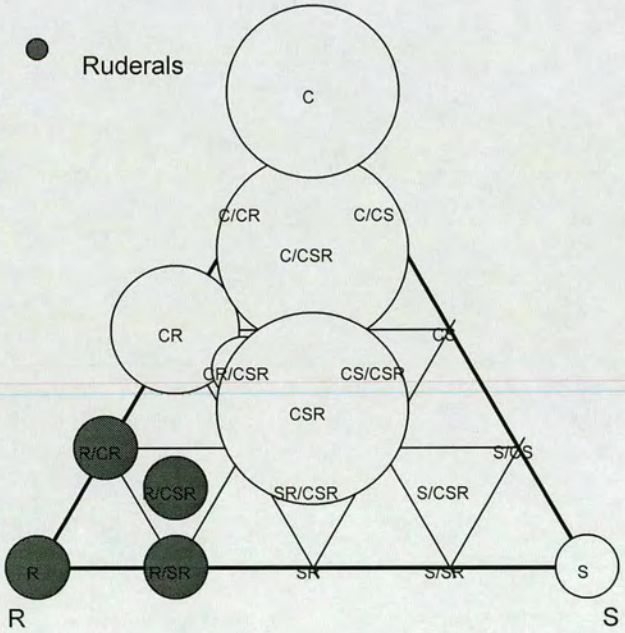
(b) British 500 data



(c) CLT


Ruderals
C
C/CR
C/CS
C/CSR
CR
CS
CR/CSR
CS/CSR
CSR
R/CR
S/CS
R/CSR
SR/CSR
S/CSR
R
R/SR
SR
S/SR
S
S

(d) DNT


Ruderals
C
C/CR
C/CS
C/CSR
CR
CS
CR/CSR
CS/CSR
CSR
R/CR
S/CS
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S/CSR
R
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SR
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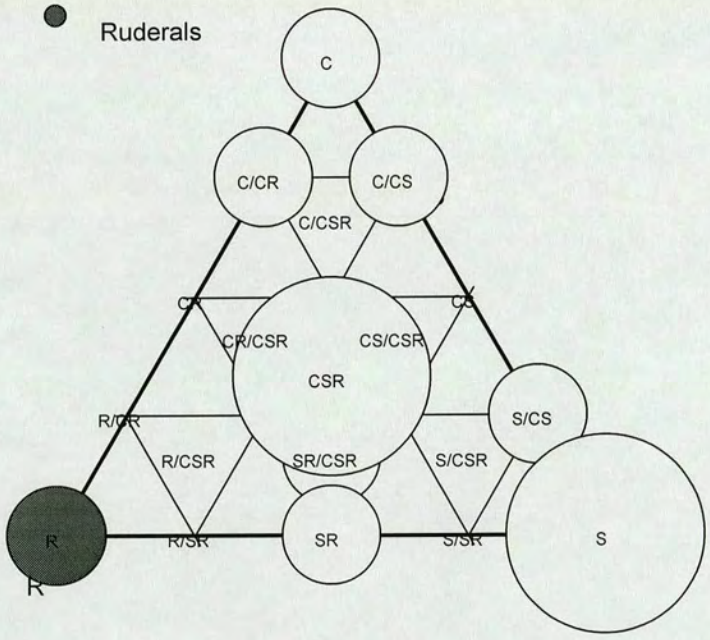
S
R
S

(e) MBT


Ruderals
C
C/CR
C/CS
C/CSR
CR/CSR
CS/CSR
CSR
S/CS
R/CR
R/CSR
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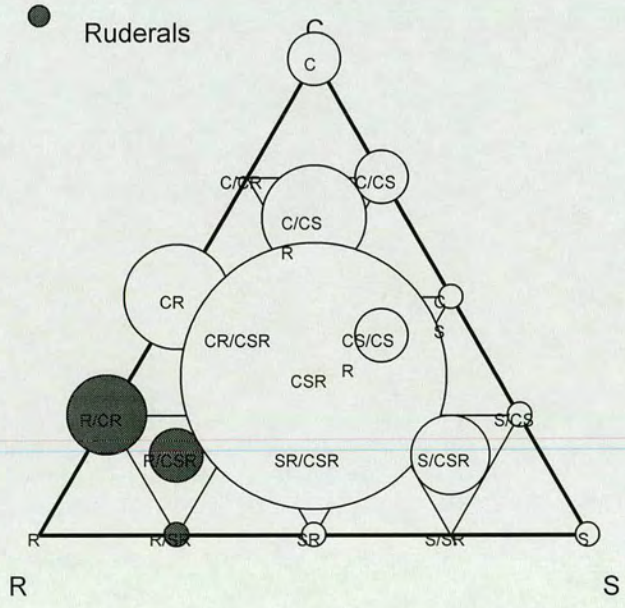
S/SR
S
R

(f) OBT


Ruderals
C
C/CR
C/CS
C/CS
R
CR
CR/CSR
CS/CS
R
CSR
R/CR
S/CS
R/CSR
SR/CSR
S/CSR
R
R/SR
SR
S/SR
S
R
S

Appendix 10 Description of matching coefficients used in ComKey

Summary comparison of methods, definitions of each of the selected types of matching coefficients and worked examples of the calculations used for both community data and relevé data. The summary, descriptions and examples were extracted from the ComKey Help file (Legg, unpublished).

Summary comparison of methods

Coefficient	Relev	Comm	Qual	Quant	Complete	Incomp	Good?
Matching species	y	y	y		y	y	+
Weighted sp match	y	y	y		y	y	++
Mountford's index	y	y	y		y	?	+
Sørensen's index	y	y	y		y		+
Presence wt match	y			*	y	y	+++
Composit satisf	y			*	y		
Dominance satisf	y			*	y		
Dominance const	y			***	y	y	
Hill's G	y			***	y		+
Czekanowski's		y		**	y		+
Matched freq		y		**	y	y	++
Freq wt match		y		**	y	y	+++

Relev: Suitable for use with individual relevés; **Comm**: Suitable for use with communities; **Qual**: Qualitative - does not make use of species abundance or frequency; **Quant**: Quatitative - * uses presence class in the type community, ** uses presence class of both type community and sample, *** uses cover abundance in relevé data and presence class in type; **Complete**: suitable for complete species lists; **Incomp**: suitable for incomplete species lists; **Good?**: + useful, ++ good, +++ recommended, ++++ best (but slow).

Presence-weighted was selected because it is designed to gauge similarity for single relevés and can be used with incomplete data. This was combined with **Matching species,** the simplest of the coefficients to use. However, these are unpublished methods. In order to give scores based on published methods **Hill's G** was selected (Hill 1989), because it is designed for use with single relevés and quantitative data. **Dominance constancy** was the third coefficient selected (Hill, 1989), again because it is designed for use with quantitative data from single relevés.

Definition of the Coefficients

The following terms are used to define the matching coefficients:

S = number of species in sample
C = number of species in community
B = number of species that occur in both sample and community
sw = species weight for species that occur in the sample
bw = species weight for species that occur in both sample and community
bp = community presence values of species occurring in both samp & comm.
bd = absolute difference between presence value in sample and presence value in community
bm = minimum of the abundance in the sample and community

Matching Species: Counts the number of species in the sample that also occur in the community. Suitable for both releves and communities where abundance is not important. Missing species are not considered, so this index is suitable for incomplete data sets. (IncQual)
= B / S

Presence-Weighted Similarity: Sum of community presence values for the species that occur in both the sample and the community, divided by 5 * number of species in sample. This will give 100 for community containing all S species with presence class 5, or 20 for all species present with presence class 1. The score is thus heavily weighted towards the most frequent species. Suitable for community or releve data. Suitable for incomplete lists. (IncQual)

= sum(bp) / 5*S * 100

Dominance Constancy: Tests if the most abundant species in the sample have a high constancy in the community. Calculates a mean of the constancy value which is weighted by the ranked abundance of the species. Suitable for single relevé data. Suitable for incomplete complete data. Takes Community presence-class into account, and the four species with highest cover-abundance in the sample (IncQuant). Described in Hill 1989 Vegetatio 83: 187-194.

Hill's G: A combination of Compositional Satisfaction, Dominance Satisfaction and Dominance Constancy weighted. (CompQuant). Described in Hill 1989 Vegetatio 83: 187-194.

$$0.5*CS + 0.25*DS + 0.25*DC$$

Example of Calculations used in Matching Coefficients - **Relevés**

Examples of the calculation of the matching coefficients used to compare relevé data with a community type from the standard classification. Species weights are the mean presence value of the species in the NVC database in communities where the species is present.

Species	Sample Domin	NVC type: A16b	Matching spp	Species weight	Matching weights	Matching presence values
Callitriche platyc.	1	-	0	1.40	-	-
Potamogeton pec.	3	V	1	2.04	2.04	5
Potamogeton nat.	3	-	0	2.09	-	-
Ceratophyllum dem.	5	I	1	1.72	1.72	1
Callitriche stagnalis	8	V	1	1.51	1.51	5
Lemna minor	-	II	-	-	-	-
Myriophyllum spic.	-	I	-	-	-	-
Sum			3	8.76	5.27	11

Number of species in sample	= s	= 5
Matching Species	= 3 / s	= 3/5
Weighted Matches	= 100 * 5.27 / 9.95	= 60.16
Presence-Weighted Matches	= 100 * 11 / (5 * s)	= 44.00

Example of Calculations used in Matching Coefficients - **Communities**

Examples of the calculation of the matching coefficients used to compare community data with a community type from the standard classification. Species weights are the mean presence value of the species in the NVC database in communities where the species is present.

Species	Sample Presence	NVC type: A16b	Lesser presence value	d for species in both sample & community	5-|d|	Species weight	(5-|d|)*wt
Callitriche plat.	I	-	0	1	-	1.40	-
Potamogeton pec.	III	V	3	-2	3	2.04	6.12
Potamogeton nat.	III	-	0	3	-	2.09	-
Ceratophyllum de.	IV	I	1	3	2	1.72	3.44
Callitriche stag.	V	V	5	0	5	1.51	7.55
Lemna minor	-	II	0	-	-	-	-
Myriophyllum spi.	-	I	0	-	-	-	-
Sum	16	14	9		10	8.76	17.11

Number of species in sample	= s	= 5
Matching Species	= 3 / s	= 3/5
Czekanowski Coeff.	= 100 * 2 * 9 / (16 + 14)	= 60.00
Matched Frequencies	= 100 * S(5 - |d|) / (5 * s)	= 40.00
Frequency-weighted Sim	= 100 * 17.11/ (5*8.76)	= 39.1

Number of species:

	Present in type	Absent in type	Total
Present in sample	B = 3	2	S = 5
Absent in sample	2	-	-
Total	C = 5	-	-

Sørensen's coefficient = 100 * 2B / (C+S) = 100 * 2 * 3 / (5 + 5) = 60

Appendix 11 The closest NVC matches for all baseline quadrats

The closest NVC community types allocated by ComKey to each of the 340 quadrats using three matching coefficient methods; Dominance constancy, Hill's G and Presence weighted and species match (combination)

Releve	Dominance Constancy	Hill's G	Presence weighted/ species match	Releve	Dominance Constancy	Hill's G	Presence weighted/ spp match
GDT1	CG1	CG4	CG2	ASB8	H18	U4	MG4
DNB10	CG1	SD7	SD7	ASM12	H18	MG5	MG4
GDP12	CG10	MG4	MG4	AST16	H18	H18	MG4
MBM1	CG10	CG10	MG5	OBB1	H18	MG5	MG4
OBT11	CG2	MG5	MG4	OBM6	H18	U16	MG4
OBT13	CG2	MG5	MG4	OBM8	H18	MG8	MG4
CLM4	CG2	CG7	OV23	OBT5	H18	MG5	MG4
DNM10	CG4	CG4	MG1	ASM2	H18	H18	MG5
GDP4	CG4	MG1	MG5	AST12	H18	U4	MG5
GDP11	CG7	H6	CG2	OBB2	H18	MG5	MG5
GDP3	CG7	CG8	CG2	OBB3	H18	MG5	MG5
GDT10	CG7	CG8	CG2	OBB8	H18	CG2	MG5
GDT3	CG7	CG7	CG2	ASH4	H18	W24	MG6
GDB4	CG7	MG5	MG5	OBM4	H18	W16	MG6
CLB10	CG7	MG1	MG9	MBB1	H18	W16	OV27
GDT19	CG7	SD7	SD1	AST1	H18	U16	U18
DNB3	CG7	W19	W11	ANT9	H18	H18	U21
GDP20	CG8	CG8	CG2	MB5	H18	H18	U21
GDT5	CG8	CG4	CG4	OBM7	H18	U16	W16
GDB9	CG8	MG4	MG1	ANM11	H18	W11	W17
GDP14	CG8	CG8	MG3	MBF8	H18	H18	W17
ANB9	CG8	MG1	MG4	MBM10	H18	U4	W17
GDP6	CG8	MG5	MG5	GDT7	H21	H6	CG2
GDT16	CG8	CG2	MG5	ANT6	H21	H12	H16
ANT7	H1	U5	H21	AST14	H21	H21	H21
ANT8	H1	H22	H21	ASM1	H21	U4	MG1
ANM9	H1	U17	W20	CLB16	H21	W17	MG1
MBT2	H11	H11	CG7	GDB23	H21	H21	MG1
MB4	H11	W23	SD7	GDP18	H21	U4	MG1
MBM2	H11	SD12	U1	GDP19	H21	MG1	MG1
DSB7	H12	MC9	MG5	ASB1	H21	H21	MG2
ANT10	H18	H12	H16	ANT13	H21	MG5	MG4
OBM10	H18	U4	MC9	DSB9	H21	MG4	MG4
ASM15	H18	U4	MG1	ASB6	H21	H21	MG5
ASB2	H18	H18	MG2	AST11	H21	U4	MG5
ASM8	H18	W17	MG2	DSB10	H21	MG4	OV23
MBB8	H18	MG2	MG2	ASM3	H21	H21	U4
ANM7	H18	U4	MG3	ASM4	H21	H21	W16
ASM16	H18	U4	MG3	DSB6	H21	MG9	W24
ASM17	H18	M22	MG3	ANT2	H22	H12	W17
MBF3	H18	MG8	MG3	GDP13	H6	H6	CG2
ASB3	H18	MG4	MG4	GDP8	H6	H6	CG2
ASB7	H18	W11	MG4	GDP9	H6	H6	CG2

Releve	Dominance Constancy	Hill's G	Presence weighted/ species match	Releve	Dominance Constancy	Hill's G	Presence weighted/ spp match
GDT6	H6	H6	CG7	MBF5	MC9	MG8	MG5
DNM4	H6	H6	H7	MBF9	MC9	MG8	MG5
DNB7	H6	CG4	MG1	OBT7	MC9	MG4	MG5
CLM14	H6	MG4	MG9	ASM11	MC9	MG4	MG8
GDT12	H7	U1	CG2	ASM6	MC9	MC9	MG8
GDT15	H7	CG4	CG2	AST4	MC9	MG8	MG8
GDT18	H7	CG8	CG2	MBB12	MC9	SD12	OV27
GDT9	H7	H6	CG2	DSB4	MC9	MG8	OV36
GDP10	H7	CG4	CG7	ASM14	MC9	U4	SD12
GDT24	H7	H6	H7	GDT20	MC9	MC10	SD8
GDT8	H7	H6	H7	MBB2	MC9	MC9	W16
MBT3	H7	U13	H7	OBB4	MC9	MC9	W24
DNB2	H7	H6	MG1	DNB5	MG1	MG5	CG2
DNT2	H7	H7	MG1	GDT4	MG1	MG2	CG8
CLB19	H7	CG4	MG1	ANB8	MG1	MG1	MG1
DNM9	H7	H6	MG2	AST15	MG1	MG1	MG1
DNT8	H7	W24	MG2	AST5	MG1	W24	MG1
GDP17	H7	CG8	MG3	DNM8	MG1	MG2	MG1
ASM10	H7	MG9	MG4	CLB6	MG1	MG1	MG1
CLM15	H7	CG7	MG4	GDB22	MG1	MG1	MG1
GDP16	H7	H7	MG4	GDB5	MG1	MG1	MG1
CLB12	H7	MC9	MG5	GDB6	MG1	MG1	MG1
GDP1	H7	CG2	MG5	MBB14	MG1	MG1	MG1
GDP2	H7	CG4	MG5	GDB7	MG1	MG2	MG2
GDP5	H7	CG8	MG5	MBB15	MG1	MG4	MG3
DNT3	H7	MG5	SD7	ANM4	MG1	MG5	MG4
GDT17	H7	U1	U1	ASB9	MG1	MG2	MG4
GDT23	H7	MG8	U1	ASM7	MG1	MG4	MG4
MBM4	H7	H7	U4	GDP7	MG1	MG1	MG5
MBM3	H7	MG5	W24	DNP10	MG1	W24	OV9
ANM1	M26	MG2	MG2	MBB6	MG1	MG2	W16
MBF2	M26	SD12	W11	GDB1	MG1	MG1	W24
ANB2	M33	MG9	M26	GDB21	MG1	W24	W24
MBB4	M33	MG9	MG1	GDB3	MG1	MG1	W24
MBB13	M4	M26	MG5	DSB11	MG10	MG4	MG4
CLB14	MC11	MG7D	MG1	DSB8	MG10	MG10	MG4
GDB15	MC4	MG5	MG5	ASM9	MG10	MG10	MG8
OBB5	MC9	CG4	CG2	ANM5	MG10	MG9	MG9
ANB4	MC9	MG4	MG1	CLB	MG10	MG4	MG9
CLB7	MC9	MG9	MG1	CLM13	MG10	MG10	OV9
ANT1	MC9	MC9	MG4	ANB12	MG2	MG2	M22
ANT11	MC9	MG4	MG4	OBB7	MG2	MG2	MG1
ASH1	MC9	MG4	MG4	DNB1	MG2	MG2	MG2
ANB6	MC9	MG4	MG5	DNT4	MG2	MG2	MG2
ASH2	MC9	MG1	MG5	DNT5	MG2	MG2	MG2
AST6	MC9	MG5	MG5	MBB5	MG2	MG2	MG2
CLB11	MC9	MG3	MG5	GDB25	MG2	MG5	MG5

Releve	Dominance Constancy	Hill's G	Presence weighted/ species match	Releve	Dominance Constancy	Hill's G	Presence weighted/ spp match
MBM9	MG2	MG2	MG5	DNP7	OV12	OV15	OV15
DNT6	MG2	OV15	OV27	DNT9	OV12	OV15	OV27
OBT2	MG3	MG5	MG3	CLM20	OV12	OV3	OV3
AST9	MG3	MG8	MG4	CLT10	OV12	OV12	OV7
OBT9	MG3	MG5	MG4	DNT10	OV15	OV15	MG6
ASB4	MG3	MG4	W10	CLT11	OV15	OV15	OV13
ASM5	MG4	MG4	MG4	CLT9	OV16	OV7	OV13
GDB10	MG4	MG4	MG4	CLT3	OV17	OV13	OV33
GDT14	MG4	MG4	MG4	AST17	OV19	OV19	OV19
ASB5	MG4	MG5	MG5	DNP4	OV20	OV15	OV15
ASM13	MG4	MG5	MG5	DNP6	OV20	OV20	MG1
GDT2	MG4	MG5	MG5	DNP8	OV20	OV20	MG2
ANT15	MG5	MG5	MG4	DNP5	OV20	OV20	OV15
ASH3	MG5	MG5	MG4	CLM1	OV22	OV11	OV15
GDB12	MG5	MG4	MG4	ANB3	OV24	OV24	MG1
GDT25	MG5	MG5	MG4	GDB18	OV24	OV3	OV17
OBT6	MG5	MG5	MG4	OBB6	OV24	W24	W24
ANT5	MG5	MG5	MG5	ANB7	OV25	W24	MG1
AST2	MG5	MG5	MG5	DNM1	OV25	MG11	MG6
GDB14	MG5	MG5	MG5	CLB8	OV25	OV8	OV13
GDB16	MG5	MG5	MG5	DNT7	OV25	OV25	OV25
MB1	MG5	SD12	U17	CLM5	OV25	MG6	OV33
GDB13	MG5	MG5	W24	DNP2	OV25	W24	OV9
DSB2	MG6	MG1	MG1	DNP3	OV25	W24	OV9
CLB13	MG6	MG5	MG3	OBB10	OV26	OV26	MG2
AST8	MG6	MG8	MG8	GDT11	OV27	H6	CG2
OBT10	MG7B	MG6	MG4	DNB9	OV27	W24	MG1
OBT3	MG7B	MG7B	MG4	DNT1	OV27	OV25	MG1
DSB5	MG8	MG7B	MG10	OBM5	OV27	MG8	MG4
MBM6	MG8	MG8	MG10	DNM2	OV27	W6	OV23
OBT1	MG8	MG8	MG3	DNM5	OV27	MG4	OV23
OBT12	MG8	MG5	MG3	DNM3	OV27	W24	OV25
OBT4	MG8	MG3	MG3	DNP	OV27	W24	OV25
ASH7	MG8	MG8	MG4	ANB10	OV27	OV24	OV27
AST10	MG8	MG8	MG4	GDB20	OV27	S1	OV27
ANB1	MG8	MG5	MG5	MBM8	OV27	MG5	OV27
ASH10	MG8	MG6	MG5	GDT13	OV27	H6	SD8
ASH9	MG8	MG5	MG5	DNB6	OV27	W11	W11
CLM12	MG8	MG8	MG5	CLB15	OV27	W24	W24
OBM9	MG8	MG5	MG5	GDB2	OV27	W24	W24
OBT8	MG8	MG5	MG5	DSB3	OV28	OV8	OV19
ASH6	MG8	W24	MG6	MBM5	OV28	OV27	OV27
AST7	MG8	MG8	MG8	MBB11	OV28	MG10	U1
CLB21	MG8	MG7B	OV6	CLB5	OV3	OV3	MG4
CLB2	MG8	MG8	SD8	ASH5	OV3	OV3	MG6
OBB9	MG9	MG9	MG9	CLM8	OV3	OV12	OV12
CLT4	OV11	OV8	OV33	CLB4	OV3	MG6	OV15

Releve	Dominance Constancy	Hill's G	Presence weighted/ species match	Releve	Dominance Constancy	Hill's G	Presence weighted/ spp match
CLB3	OV3	OV12	OV19	DNB4	U5	SD12	W11
CLM17	OV3	OV17	OV19	MBF7	U5	H18	W11
CLM2	OV3	OV3	OV3	GDP15	U6	CG10	MG3
CLM3	OV3	OV3	OV33	DNM6	W11	MG5	MG1
CLB9	OV3	OV3	OV6	MBB7	W11	MG2	MG2
CLT8	OV33	OV11	OV13	AST13	W11	U13	MG5
CLB20	OV36	M28	MG8	AST3	W11	W11	W11
CLT7	OV36	OV36	OV8	ANT16	W11	W23	W24
GDB11	OV38	MG1	MG1	ANB11	W12	MG4	MG2
GDB8	OV38	MG1	MG1	ANM6	W12	MG3	MG4
GDB24	OV38	MG1	MG2	MBB3	W14	W24	OV27
OBM1	OV38	OV38	MG2	CLB17	W18	MG1	MG1
CLT5	OV5	OV5	OV11	CLB18	W18	W17	MG1
CLB22	OV5	OV4	OV3	ANM2	W23	MG1	MG1
CLM10	OV5	OV9	OV9	DNB8	W23	MG4	MG1
CLT6	OV6	OV14	OV13	DNM7	W23	W24	MG1
CLM18	OV6	OV6	OV13	ANM10	W23	MG2	W11
CLM6	OV6	OV13	OV13	OBM3	W24	W23	W6
CLM16	OV7	OV3	OV10	ASB10	W7	W7	MG2
CLM9	OV7	OV7	OV11	GDB17	no species in quadrat		
CLM7	OV7	OV13	OV15				
CLM11	OV7	OV7	OV36				
ASH8	OV7	OV3	SD8				
CLM19	OV9	OV12	OV12				
DNP9	OV9	OV8	OV9				
CLT1	SD1	OV33	OV13				
CLT2	SD1	OV9	OV13				
ANT3	SD8	MG5	MG5				
MBM7	U1	MG10	OV27				
GDT21	U11	U11	OV2				
GDT22	U11	U11	U11				
MBF6	U13	U13	MG3				
DSB1	U17	MG9	MG6				
MBF1	U17	U17	U17				
ANM8	U17	U17	W11				
OBM2	U18	U16	MG1				
MBB9	U18	MG9	MG3				
MBF4	U18	U16	MG3				
ANB5	U18	MG9	MG9				
ANM3	U20	U16	MG1				
GDB19	U20	SD7	W10				
ANT4	U20	U20	W16				
MBB10	U4	SD12	U1				
MBF10	U5	SD12	MG3				
ANT14	U5	MG5	MG4				
ANT12	U5	U4	MG5				

Appendix 12 Quadrats by TWINSPAN grouping

The quadrats allocated to each of the 28 TWINSPAN grouping are displayed in six columns. The heavy line after group 15 marks the first division.

group	quadrat	group	quadrat	group	quadrat	group	quadrat	group	quadrat	group	quadrat
00000	MBT4	00010	GDB23	00100	ASM1	00110	CLB7	01001	GDT4 10	10100	CLT2
00000	MBT5	00010	GDB25	00100	ASM2	00110	CLB10	01010	MB2 11	10100	CLM7
00000	MBM2 1	00010	GDP18	00100	ASM3	00110	CLB11	01100	DNM8	10100	CLM14
00001	MBB1	00010	GDP19	00100	ASM6	00110	CLB12	01100	CLB16	10100	CLM16
00001	MBM10 2	00010	MBB3	00100	ASM11	00110	CLB13	01100	GDB7	10100	CLM17
00010	ANB1	00010	MBB4	00100	ASM17	00110	CLB14	01100	GDB9	10100	CLM18
00010	ANB2	00010	MBB5	00100	AST2	00110	DSB1	01100	GDB13	10100	CLM19
00010	ANB3	00010	MBB6	00100	AST4	00110	DSB2	01100	GDB24 12	10100	CLM20 20
00010	ANB4	00010	MBB8	00100	AST5	00110	DSB3	01101	DNB1	10101	CLT3
00010	ANB5	00010	MBB9	00100	AST6	00110	DSB5	01101	DNB2	10101	CLT4
00010	ANB6	00010	MBB14	00100	AST7	00110	DSB6	01101	DNB3	10101	CLT5
00010	ANB7	00010	OBB4	00100	AST8	00110	DSB7	01101	DNB4	10101	CLT6
00010	ANB8	00010	OBB6	00100	AST9	00110	DSB8	01101	DNB5	10101	CLT7
00010	ANB9	00010	OBB7	00100	AST11	00110	DSB9	01101	DNB6	10101	CLT8
00010	ANB10	00010	OBB10	00100	AST13	00110	DSB10	01101	DNM10 13	10101	CLT9
00010	ANB11	00010	OBM1	00100	AST17	00110	DSB11	01110	DNB10	10101	CLT10
00010	ANB12	00010	OBM2	00100	MBF3	00110	CLM12	01110	DNM3	10101	CLT11
00010	ANM1	00010	OBM6	00100	MBF9	00110	GDB14 7	01110	DNM9	10101	CLM6
00010	ANM2	00010	OBM10 3	00100	OBB9	00111	ASH8	01110	DNT2	10101	CLM9 21
00010	ANM3	00011	ANM6	00100	OBM3	00111	ASH9	01110	CLB19	10110	ASH5
00010	ANM4	00011	ANM7	00100	OBM4	00111	MBB2	01110	GDT8	10110	CLB3
00010	ANT4	00011	ANM8	00100	OBM5	00111	MBB10	01110	GDT9	10110	CLB4
00010	ANT16	00011	ANM9	00100	OBM8	00111	MBB11	01110	GDT13	10110	CLB8
00010	ASB1	00011	ANM10	00100	OBM9 5	00111	MBB15	01110	GDT14	10110	CLB21
00010	ASB2	00011	ANM11	00101	ANT3	00111	MBM1	01110	GDT18 14	10110	CLM1
00010	ASB3	00011	ANT2	00101	AST10	00111	MBM6	01111	DNB7	10110	CLM2
00010	ASB4	00011	ANT5	00101	OBB1	00111	MBM7 8	01111	DNB8	10110	CLM3
00010	ASB5	00011	ANT6	00101	OBB2	01000	GDB12	01111	DNB9	10110	CLM4
00010	ASB6	00011	ANT7	00101	OBB3	01000	GDB15	01111	DNM2	10110	CLM5
00010	ASB7	00011	ANT8	00101	OBB5	01000	GDP9	01111	DNM4	10110	CLM8 22
00010	ASB8	00011	ANT9	00101	OBB8	01000	GDP10	01111	DNM5	10111	DSB4
00010	ASB9	00011	ANT10	00101	OBT1	01000	GDP13	01111	DNM6	10111	CLM11
00010	ASB10	00011	ANT11	00101	OBT2	01000	GDT1	01111	DNM7	10111	CLM13 23
00010	ASM4	00011	ANT12	00101	OBT3	01000	GDT2	01111	GDB10 15	11000	DNP2
00010	ASM7	00011	ANT13	00101	OBT4	01000	GDT3	10000	DNM1	11000	DNP3
00010	ASM8	00011	ANT14	00101	OBT5	01000	GDT6	10000	DNT5	11000	DNP4
00010	ASM10	00011	ANT15	00101	OBT6	01000	GDT7	10000	DNT9	11000	DNP5
00010	ASM12	00011	ASM13	00101	OBT7	01000	GDT11	10000	DNT10 16	11000	DNP6
00010	ASM15	00011	ASM14	00101	OBT8	01000	GDT12	10001	DNT1	11000	DNP7
00010	ASM16	00011	AST3	00101	OBT9	01000	GDT15	10001	DNT7	11000	DNP8
00010	AST1	00011	AST12	00101	OBT10	01000	GDT16	10001	CLB9	11000	DNP9
00010	AST14	00011	AST16	00101	OBT11	01000	GDT23 9	10001	CLM15	11000	DNP10 24
00010	AST15	00011	MBT1	00101	OBT12	01001	GDP1	10001	GDB18 17	11001	DNP1
00010	CLB15	00011	MBB7	00101	OBT13 6	01001	GDP2	10010	GDB16	11001	DNT4
00010	CLB17	00011	MBB13	00110	ANM5	01001	GDP3	10010	GDT10	11001	DNT6
00010	CLB18	00011	MBF1	00110	ANT1	01001	GDP4	10010	GDT24	11001	DNT8
00010	GDB1	00011	MBF2	00110	ASH1	01001	GDP5	10010	GDT25 18	11001	GDT20 25
00010	GDB2	00011	MBF4	00110	ASH2	01001	GDP6	10011	CLB20	11010	GDB20
00010	GDB3	00011	MBF5	00110	ASH3	01001	GDP7	10011	CLM14	11010	GDT19
00010	GDB4	00011	MBF6	00110	ASH4	01001	GDP8	10011	GDT5	11010	MBB12
00010	GDB5	00011	MBF7	00110	ASH6	01001	GDP11	10011	GDT17	11010	MBM8 26
00010	GDB6	00011	MBF8	00110	ASM5	01001	GDP12	10011	MBT3	11011	DNT3 27
00010	GDB8	00011	MBF10	00110	ASM9	01001	GDP14	10011	MBM3	111--	GDT21
00010	GDB11	00011	MBM9	00110	CLB1	01001	GDP15	10011	MBM4	111--	GDT22 28
00010	GDB19	00011	OBM7 4	00110	CLB2	01001	GDP16	10011	MBM5 19		
00010	GDB21	00100	ASH7	00110	CLB5	01001	GDP17	10100	CLB22		
00010	GDB22	00100	ASH10	00110	CLB6	01001	GDP20	10100	CLT1		

Appendix 13 Species by TWINSPAN grouping

The species allocated to the main TWINSPAN groupings are displayed in three collumns The species names are abbreviated to the first three letters of the generic name followed by the first three letters of the specific name. The exceptions are Rumex acetosa and R. acetosella whose species names are written in full.

species	code		species	code		species	code	
CHAANG	00000		ACHMIL	01100	3rd	EPIMON	10000	1st
LINVUL	00000		AGRSTO	01100		URTDIO	10000	
SENJAC	00000		BRYPAL	01100		CIRARV	10100	3rd
TUSFAR	00100	3rd	DACFUC	01100		EPIHIR	10101	
FESOVI	00100		DESFLE	01100		MEDLUP	10101	
HOLMOL	00100		LOTCOR	01100		RUMCRI	10101	
LEUVUL	00100		LUPNOO	01100		CIRVUL	10110	
LINCAT	00100		ODOVER	01100		RANREP	10110	
HOLLAN	01000	2nd	POATRI	01100		ARCMIN	11000	2nd
PLALAN	01000		PRUVUL	01100		CERFON	11000	
TAROFF	01000		RANACR	01100		POTSP	11000	
TRIREP	01000		RHIMIN	01100		RUMOBT	11100	3rd
ARRELA	01010		RUMacetosa	01100		CERGLO	11101	
CENNIG	01010		SANMIN	01100		MATDIS	11101	
CRAMON	01010		TRIPRA	01100		MYOARV	11101	
FRAVES	01010		VICHIR	01100		PERMAC	11101	
HYPRAD	01010		AGRGIG	01101		POLAVI	11101	
PILOFF	01010		ALNGLU	01101		RESLUT	11101	
BETPEN	01011		ANGSYL	01101		SENVIS	11101	
DACGLO	01011		ANTODO	01101		SENVUL	11101	
EUPNEM	01011		ANTSYL	01101		SONASP	11101	
HERSPH	01011		CALVUL	01101		STEMED	11101	
HYPCUP	01011		CLAFIM	01101		TRIINO	11101	
ROSCAN	01011		CYNCRI	01101		VERSER	11101	
SALCAP	01011		CYTSCO	01101		ARESER	11110	
TRICAM	01011		HYPJUT	01101		SAGPRO	11111	
			LATPRA	01101				
3rd level break at top of next collumn			LOPCUS	01101				
			PELCAN	01101				
			POLCOM	01101				
			POTERE	01101				
			PTEAQU	01101				
			RHYSQU	01101				
			RUBFRU	01101				
			RUBIDA	01101				
			SORAUC	01101				
			VICCRA	01101				
			DESCES	01110				
			EQUARV	01110				
			GALAPA	01110				
			POANEM	01110				
			POLJUN	01110				
			RUMacetosella	01110				
			POAANN	01111				
			1st level break at top of next collumn					

Appendix 14 NVC community types by TWINSPAN grouping

The NVC community types allocated to each quadrat by ComKey are by TWINSPAN grouping

group	NVC type	group	NVC type	group	NVC type	group	NVC type
00000	U1	00010	W10	00011	W10	00101	MG1
00000	U1	00010	W10	00011	W10	00101	MG1
00000	W17 1	00010	W10	00011	W10	00101	MG1
00001	U1	00010	W10	00011	W15	00101	MG1
00001	W11 2	00010	W23	00011	W16	00101	MG1
00010	CG2	00010	W24	00011	W17	00101	MG1
00010	CG4	00010	W24	00011	W17	00101	MG1
00010	M22	00010	W24	00011	W17	00101	MG1
00010	M27	00010	W24	00011	W17	00101	MG1
00010	MG1	00010	W24	00011	W17	00101	MG9
00010	MG1	00010	W24	00011	W17	00101	SD8
00010	MG1	00010	W24	00011	W17	00101	U4
00010	MG1	00010	W24	00011	W4	00101	U4
00010	MG1	00010	W24	00011	W4	00101	U4 6
00010	MG1	00010	W6	00011	W4	00110	CG2
00010	MG1	00010	W8	00011	W4 4	00110	CG3
00010	MG1	00010	W8	00100	CG10	00110	CG3
00010	MG1	00010	W8	00100	CG10	00110	CG4
00010	MG1	00010	W8	00100	CG10	00110	M22
00010	MG1	00010	W8	00100	CG2	00110	MG1
00010	MG1	00010	W8	00100	CG2	00110	MG1
00010	MG2	00010	W8	00100	MG1	00110	MG1
00010	MG4	00010	W8	00100	MG1	00110	MG1
00010	OV24	00010	W9	00100	MG3	00110	OV10
00010	OV26	00010	W9	00100	MG6	00110	OV10
00010	OV27	00010	W9	00100	OV23	00110	OV10
00010	OV27	00010	W9 3	00100	SD8	00110	OV10
00010	S25	00011	CG10	00100	U1	00110	OV10
00010	SD12	00011	CG10	00100	U1	00110	OV10
00010	SD7	00011	CG10	00100	U17	00110	OV10
00010	SD7	00011	CG10	00100	U4	00110	OV27
00010	SD7	00011	CG10	00100	U4	00110	SD8
00010	SD8	00011	CG10	00100	U4	00110	SD8
00010	U1	00011	CG2	00100	U4	00110	SD8
00010	U4	00011	CG2	00100	U4	00110	SD8
00010	W10	00011	MC9	00100	U4	00110	SD8
00010	W10	00011	MG1	00100	U4	00110	SD8
00010	W10	00011	MG9	00100	W10	00110	U4
00010	W10	00011	SD7	00100	W10	00110	U4
00010	W10	00011	SD8	00100	W10	00110	U4
00010	W10	00011	SD8	00100	W24	00110	U4
00010	W10	00011	SD8	00100	W24 5	00110	W10
00010	W10	00011	U1	00101	CG2	00110	W24
00010	W10	00011	U1	00101	CG3	00110	W24
00010	W10	00011	U1	00101	MG1	00110	W24 7
00010	W10	00011	U17	00101	MG1	00111	MG1
00010	W10	00011	U4	00101	MG1	00111	MG4
00010	W10	00011	U4	00101	MG1	00111	SD8

group	NVC type	
00111	SD8	
00111	U1	
00111	U1	
00111	U1	
00111	U1	
00111	W1	8
01000	CG2	
01000	CG2	
01000	CG2	
01000	CG2	
01000	CG2	
01000	CG3	
01000	MG1	
01000	SD8	
01000	SD8	
01000	SD8	
01000	SD8	
01000	SD8	
01000	SD8	
01000	SD8	
01000	U1	9
01001	CG2	
01001	CG2	
01001	CG2	
01001	CG2	
01001	CG2	
01001	CG3	
01001	MG1	
01001	MG1	
01001	MG1	
01001	SD8	
01001	SD8	
01001	SD8	
01001	SD8	
01001	SD8	
01001	SD8	10
01010	CG7	11
01100	CG3	
01100	OV23	
01100	SD7	
01100	W10	
01100	W9	
01100	W9	12
01101	MG1	
01101	OV23	
01101	SD8	
01101	SD8	
01101	SD8	
01101	W17	
01101	W4	13
01110	CG2	

group	NVC type	
01110	MG1	
01110	MG1	
01110	MG1	
01110	MG1	
01110	OV10	
01110	OV23	
01110	OV23	
01110	SD7	
01110	U1	14
01111	MG1	
01111	MG1	
01111	MG1	
01111	MG1	
01111	OV23	
01111	OV23	
01111	OV27	
01111	OV27	
01111	W8	15
10000	OV10	
10000	OV9	
10000	OV9	
10000	SD1	16
10001	OV10	
10001	OV10	
10001	OV23	
10001	OV25	
10001	OV9	17
10010	CG2	
10010	CG3	
10010	OV10	
10010	SD8	18
10011	M6	
10011	OV10	
10011	OV10	
10011	SD8	
10011	SD8	
10011	W10	
10011	W24	
10011	W24	19
10100	OV10	
10100	OV10	
10100	OV10	
10100	OV10	
10100	OV3	
10100	OV4	
10100	OV4	
10100	OV6	20
10101	OV10	
10101	OV10	
10101	OV10	

group	NVC type	
10101	OV10	
10101	OV33	
10101	OV33	
10101	OV4	
10101	OV9	
10101	OV9	
10101	OV9	21
10110	OV10	
10110	OV10	
10110	OV10	
10110	OV10	
10110	OV10	
10110	OV10	
10110	OV10	
10110	OV10	
10110	OV10	
10110	OV4	22
10111	OV10	
10111	OV10	
10111	OV10	23
11000	OV10	
11000	OV10	
11000	OV9	
11000	OV9	
11000	OV9	
11000	SD1	
11000	SD1	
11000	U1	
11000	W21	24
11001	OV15	
11001	OV27	
11001	OV9	
11001	OV9	
11001	SD8	25
11010	OV20	
11010	SD1	
11010	SD1	
11010	U1	26
11011	SD1	27
111--	U1	
111--	U11	28

Appendix 15 Chemical analysis results

Analysis of surface (sur) and subsoil (sub) samples from Greendykes (GD), Mid Breich (MB), Oakbank (OB) and Clapperton (CL) bings for available Na (sodium), Mg (magnesium), K (potassium), P (phosphorous), pH (potential hydrogen), NH_4 (ammonium) and NO_3 (nitrate) in parts per million (ppm). The elevations (ele) within the sites are abbreviated.
pl = plateau, t = top slopes, m = middle slopes, b = base

site	ele	Na		Mg		K		P		Ca		pH	
		sub	sur	sub	sur	sub	sur	sub	sur	sub	sur	sub	sur
GD	pl	71.70	74.00	558.00	574.00	335.00	371.00	10.20	10.40	4440.00	4960.00	6.47	6.00
GD	pl	53.10	47.80	314.00	415.00	276.00	315.00	13.30	14.60	1200.00	1633.00	6.28	6.51
GD	pl	81.60	78.70	987.00	912.00	259.00	291.00	8.70	10.00	6300.00	5900.00	6.71	7.26
GD	pl	62.30	73.60	1289.00	933.00	220.00	272.00	8.50	10.90	13980.0	7400.00	6.88	7.21
GD	t	85.50	97.20	797.00	810.00	156.00	199.00	26.60	27.80	2686.00	6960.00	7.41	7.22
GD	t	32.20	30.10	78.40	73.80	63.00	70.00	25.90	27.00	188.00	3233.00	6.05	5.72
GD	t	63.60	67.00	454.00	454.00	263.00	303.00	18.70	17.30	1660.00	2180.00	6.40	6.20
GD	t	92.80	85.90	655.00	638.00	257.00	271.00	30.80	27.80	3117.00	1606.00	6.93	6.77
GD	m	90.00	78.40	1265.00	1020.00	186.00	227.00	6.70	7.30	2607.00	3074.00	7.28	6.91
GD	m	78.90	78.50	1206.00	1108.00	155.00	201.00	13.80	13.30	15200.0	10160.0	6.54	6.36
GD	m	93.70	100.00	387.00	393.00	74.00	86.00	128.40	118.00	2510.00	3980.00	6.52	6.24
GD	m	38.20	44.40	111.00	159.00	180.00	192.00	48.80	38.90	1805.00	3110.00	6.68	6.25
GD	b	31.80	32.20	103.00	101.00	296.00	311.00	85.20	111.20	3740.00	3140.00	6.42	6.55
GD	b	22.10	24.00	73.10	76.60	204.00	240.00	180.00	168.20	1924.00	2180.00	6.24	6.41
GD	b	29.70	30.90	71.10	73.10	114.00	129.00	109.80	105.80	1230.00	1260.00	5.91	5.99
GD	b	24.10	31.00	39.00	63.90	56.00	73.00	98.50	121.50	3000.00	1056.00	6.10	6.32
MB	t	21.80	27.00	37.20	82.40	55.00	49.00	10.80	10.30	1100.00	3710.00	5.75	5.76
MB	t	23.10	24.30	71.10	83.20	76.00	67.00	32.30	20.10	774.00	1030.00	5.73	5.80
MB	m	26.50	26.80	18.40	33.80	87.00	89.00	21.40	22.50	497.00	432.00	6.42	6.71
MB	m	31.60	28.50	15.80	20.00	89.00	113.00	12.30	10.30	81.40	341.00	6.75	6.97
MB	m	25.90	26.00	47.00	49.80	113.00	126.00	8.50	8.10	49.50	49.80	7.29	7.58
MB	m	275.20	230.40	1202.00	1159.00	49.00	73.00	34.10	28.20	20300.0	20040.0	8.09	8.02
MB	b	23.80	25.00	33.70	42.20	85.00	90.00	29.40	30.00	99.10	230.00	6.15	5.94
MB	b	32.20	38.30	81.70	118.00	163.00	195.00	10.00	9.60	282.00	619.00	6.46	6.22
MB	b	29.30	29.60	82.90	85.00	150.00	173.00	17.30	21.30	2657.00	1940.00	6.67	6.30
MB	b	15.10	13.30	102.00	96.10	143.00	172.00	30.40	31.50	2650.00	3130.00	6.25	6.48

site	ele	Na		Mg		K		P		Ca		pH		NH_4		NO_3	
		sub	sur	sub	sur	sub	sur	sub	sur	sub	sur	sub	sur	sub	sur	sub	sur
OB	t	38.18	34.52	211.10	220.36	249.84	279.00	39.47	37.92	1346.00	1364.28	6.69	6.28	0.10	0.47	0.05	1.44
OB	t	31.70	27.28	187.30	220.04	221.58	250.30	37.41	33.83	1052.88	1187.22	6.29	6.17	0.05	0.25	0.40	1.34
OB	t	30.24	25.54	222.66	245.76	288.36	276.14	38.58	32.37	1461.68	1381.44	6.16	6.34	0.13	0.45	0.05	0.61
OB	t	42.92	37.34	218.26	236.24	153.86	210.38	23.04	21.81	1433.94	1458.92	7.04	6.89	0.07	0.22	1.18	1.46
OB	m	35.68	31.96	288.28	347.12	241.98	297.90	21.48	24.41	2336.42	2646.84	7.25	6.62	0.06	0.22	1.81	4.67
OB	m	40.22	33.60	202.52	259.00	214.88	329.64	33.38	36.44	1226.84	1352.76	6.82	6.25	0.08	0.10	0.99	3.48
OB	m	20.00	14.90	211.28	223.76	105.30	119.38	22.87	22.23	1294.54	1136.04	6.91	6.41	0.16	0.41	0.15	2.03
OB	m	15.42	11.72	202.88	143.00	75.34	92.22	18.11	14.20	1052.58	650.86	6.59	6.25	0.15	0.14	0.52	1.03
OB	b	41.68	41.60	248.60	271.04	129.34	156.08	19.37	24.49	3137.76	1838.58	7.91	6.93	0.08	0.11	1.10	3.03
OB	b	44.34	39.00	213.74	191.02	242.36	187.18	40.90	28.69	1226.40	932.90	6.69	6.19	0.09	0.09	0.42	0.64
OB	b	49.74	49.00	354.98	328.84	84.26	127.36	20.26	11.35	6828.08	5797.80	7.82	7.28	0.16	0.09	0.03	1.18
OB	b	23.60	23.40	170.44	208.10	104.84	125.66	17.87	17.64	1166.80	1283.28	6.21	6.30	0.11	0.19	0.80	0.81
CL	t	5.40	4.54	135.36	184.52	11.86	12.80	4.99	7.73	3435.22	1639.94	7.69	7.71	0.15	0.10	0.29	0.61
CL	t	5.98	5.96	332.74	293.28	18.56	19.18	8.74	10.47	2138.62	3295.20	7.99	7.98	0.09	0.09	0.38	0.57
CL	t	10.32	9.40	301.58	295.92	22.36	19.00	8.62	6.74	2394.78	2253.74	7.92	7.91	0.09	0.09	0.28	0.37
CL	t	17.60	10.86	190.04	137.64	29.84	26.28	9.26	8.94	974.00	1876.22	7.92	7.80	0.08	0.08	0.48	0.66
CL	m	3.18	1.28	153.72	203.14	8.86	24.58	5.45	5.95	6729.06	1150.02	7.15	6.89	0.08	0.08	0.35	0.42
CL	m	26.38	28.48	210.92	218.38	75.86	94.06	16.43	15.82	6733.42	6956.92	8.15	8.01	0.08	0.10	0.55	0.62
CL	m	4.74	7.30	217.36	256.38	5.14	10.86	9.06	10.89	1091.16	1312.08	7.36	7.53	0.10	0.12	0.25	0.40
CL	m	35.00	40.24	280.10	291.34	88.62	93.78	13.89	15.23	7906.00	8070.80	8.06	8.17	0.07	0.08	0.39	0.48
CL	b	8.74	7.70	184.88	189.82	64.90	89.20	7.34	7.32	1455.46	1407.74	6.54	6.78	0.08	0.09	0.91	0.85
CL	b	10.30	9.20	106.66	107.46	32.66	52.10	15.57	14.78	2093.28	1853.38	6.99	7.01	0.07	0.11	1.65	2.42
CL	b	32.14	29.30	324.84	301.58	75.54	100.44	7.64	9.47	7861.58	7520.98	8.04	8.10	0.19	0.10	0.37	0.86
CL	b	37.48	37.82	300.52	291.02	100.08	120.16	14.14	15.27	8342.14	7838.68	8.12	8.17	0.08	0.10	0.53	0.79

Appendix 16 Extracts from CCA results summary log and description of calculation of explained variance

Two extracts from the summary log produced by a canonical correspondence analysis (CCA) calculated in the computer programme CANOCO as described in Chapter Five. The summary log describes the data input and calculations used to produce the graphical output presented in Figure 5.10. Each of the numbered sections of the log is described in turn (ter Braak and Šmilauer, 2002). A description follows each extract describing the calculations made to produce Table 5.7.

Species data : C:\My Documents\barbra\nine species\flowerheads.dta .....①
Covariable data : C:\My Documents\barbra\nine species\presabs.dta
Environmental data : C:\My Documents\barbra\nine species\physical.dta

Number of samples 40 .....②
Number of species 9
Number of occurrences 121
No. of covariables : 9
No. of environmental variables : 5

No interaction terms defined ..... ③
No transformation of species data
No species-weights specified
No sample-weights specified
No downweighting of rare species

**** Summary ****

Axes	1	2	3	4	Total inertia ...④
Eigenvalues :	0.230	0.109	0.019	0.012	1.330
Species-environment correlations:	0.901	0.861	0.644	0.622	.....⑤
Cumulative percentage variance					
of species data:	44.4	65.5	69.1	71.3	.....⑥
of species-environment relation:	61.8	91.2	96.2	99.3	.....⑦

Sum of all eigenvalues 0.519 ..... ⑧
Sum of all canonical eigenvalues 0.373 .....⑨

The sum of all eigenvalues is after fitting covariables. Percentages are taken with respect to residual variances i.e. variances after fitting covariables.

① the names and locations of the data files used in the calculation are identified:
Species data = number of flowerheads per species in each of the recording quadrats
Covariable data = presence or absence of each species in the recording quadrats
Environmental data = measured physical environmental variables in each of the recording quadrats.

② the number of variables within the data sets is presented:
Number of samples = 40 quadrat blocks
Number of species = 9
Number of occurrences = 121 records in the matrix of 9x40 cells
Number of covariables = 9 species, either present or absent
Number of environmental variables = 5 measured physical variables

③ defines the options selected when setting parameters of the analysis – in this example the default option were selected as the data were not transformed

④ total inertia = the total variance in the species data
eigenvalues measure the importance of each of the axes (values between 0 and 1)

⑤ species environment correlation measures the strength of the relationship between species and environment for a particular axis and it does not follow that a high correlation means that a high amount of the species data is explained by the environmental values

⑥ percentage variance of species data is given cumulatively and is derived from ⑧ the sum of all eigenvalues

⑦ percentage variance of species environment relation is given cumulatively and is derived from ⑨ the sum of all canonical eigenvalues

When a covariable is used in the CCA the difference between ④ the total inertia and ⑧ the sum of all eigenvalues is used to calculate the percentage variance in species data described by the covariable. In this example:
((1.330 – 0.519) /1.330)*100 = 60.98 (Table 5.7)

The percentage variance in species data described by the environmental variable, the physical environment, is calculated from ⑨ the sum of all canonical eigenvalues. In this example:
(0.373/1.330)*100 = 28.05 (Table 5.7)

Supplementary variables:\MyDocuments\barbra\ninespecies\chemical.dta .....①
No. of environmental variables : 6

**** Summary ****

Axes	1	2	3	4	Total inertia
Species-environment correlations:	0.910	0.923	0.652	0.681	
Cumulative percentage variance					
of species data:	44.4	65.5	69.1	71.3	
of species-environment relation:	59.0	90.7	95.5	98.9	
Sum of all eigenvalues					0.519
Sum of all canonical eigenvalues					0.398 .....⑨

The sum of all eigenvalues is after fitting covariables. Percentages are taken with respect to residual variances i.e. variances after fitting covariables.

The additional variance in species data described by ① the supplementary variable, the chemical environment, is calculated from ⑨ the sum of all canonical eigenvalues. In this example:

(0.398/1.133*100 = 29.92 (Table 5.7)